AGENCY DRAFT RECOVERY PLAN

for

Cumberland Elktoe (*Alasmidonta atropurpurea*), Oyster Mussel (*Epioblasma capsaeformis*), Cumberlandian Combshell (*Epioblasma brevidens*), Purple Bean (*Villosa perpurpurea*), and Rough Rabbitsfoot (*Quadrula cylindrica strigillata*)

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Literature citations should read as follows:

U.S. Fish and Wildlife Service. 2003. Agency Draft Recovery Plan for Cumberland Elktoe, Oyster Mussel, Cumberlandian Combshell, Purple Bean, and Rough Rabbitsfoot. Atlanta, Georgia. 176 pp.

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EXECUTIVE SUMMARY

Current Status: The Cumberland elktoe (*Alasmidonta atropurpurea*), oyster mussel (*Epioblasma capsaeformis*), Cumberlandian combshell (*Epioblasma brevidens*), purple bean (*Villosa perpurpurea*), and rough rabbitsfoot (*Quadrula cylindrica strigillata*) are federally listed as endangered species. All five mussels are native (endemic) to either the Cumberland River system (Cumberland elktoe), the Tennessee River system (purple bean and rough rabbitsfoot), or to both river systems (oyster mussel and Cumberlandian combshell). They once existed in hundreds of river miles and now survive in only a few relatively small, isolated populations. The Cumberland elktoe still exists in 12 mostly small tributaries in the upper Cumberland River system in Kentucky and Tennessee. The oyster mussel survives in one Cumberland River system tributary in Kentucky and Tennessee and five tributaries of the Tennessee River system in Tennessee and Virginia. The Cumberlandian combshell persists in five tributaries of the Cumberland and Tennessee River systems in Alabama, Kentucky, Tennessee, Virginia, and Mississippi. The purple bean is extant in five tributaries, and the rough rabbitsfoot is extant in three tributaries of the upper Tennessee River system in Tennessee and Virginia.

Habitat Requirements and Limiting Factors: These species, which are generally adapted to live in the gravel shoals of free-flowing rivers and streams, were eliminated from much of their historical ranges due to human related (anthropogenic) factors, such as impoundments (not as significant a factor for the Cumberland elktoe and purple bean), channelization, pollution, sedimentation, and other factors. The species and their habitats are currently being impacted by deteriorated water and substrate quality (primarily resulting from poor land-use practices), contaminants, and, potentially, the invasion of the nonnative zebra mussel (*Dreissena polymorpha*). Their restricted ranges and low population levels also increase their vulnerability to toxic chemical spills and the deleterious effects of genetic isolation.

Recovery Objective: Delisting.

Recovery Criteria: Downlisting from endangered to threatened status will occur when the following criteria are met for protecting extant stream populations, ensuring the viability of populations, and/or designating nonessential experimental population status (see "Part II, Recovery" for more specific streams and/or stream systems required for downlisting): (1) eight streams with distinct viable populations of the Cumberland elktoe, seven streams with distinct populations of the oyster mussel and Cumberlandian combshell, three streams with distinct viable populations of the purple bean, and two streams with distinct viable populations of the rough rabbitsfoot have been established; (2) one distinct naturally reproduced year class exists within each of a species' viable stream populations; (3) studies of the mussels' biological and ecological requirements have been completed and any required recovery measures developed and implemented from these studies are beginning to be successful, as evidenced by an increase in population density and/or an increase in the length of the river reach inhabited by the species; (4) no foreseeable threats exist that would likely impact the survival of the species over a significant portion of their ranges; (5) within larger streams the species is distributed over a long enough reach that a single catastrophic event is not likely to eliminate or significantly reduce the entire population in that stream; and (6) biennial monitoring of the five species yields the results outlined in “criterion 1”above over a 10-year period.

Delisting will occur when the following criteria are met for protecting extant stream populations, ensuring the viability of populations, and/or designating nonessential experimental population status (see “Part II, Recovery” for more specific streams and/or stream systems required for delisting): (1) 10 streams with distinct viable populations of the Cumberland elktoe, 11 streams with distinct viable populations of the oyster mussel, 10 streams with distinct viable populations of the Cumberlandian combshell, 4 streams with distinct viable populations of the purple bean, and 3 streams with distinct viable populations of the rough rabbitsfoot have been established; (2) two distinct naturally reproduced year class exists within each of a species’ viable stream populations; (3) studies of the mussels’ biological and ecological requirements have been completed and any required recovery measures developed and implemented from these studies are beginning to be successful, as evidenced by an increase in population density and/or an increase in the length of the river reach inhabited by the species; (4) no foreseeable threats exist that would likely impact the survival of the species over a significant portion of their ranges; (5) within larger streams the species is distributed over a long enough reach that a single catastrophic event is not likely to eliminate or significantly reduce the entire population in that stream; and (6) biennial monitoring of the five species yields the results outlined in “criterion 1”above over a 10-year period.

Actions Needed:

1. Utilize existing legislation/regulations to protect current and newly discovered populations.

2. Determine the species’ life history requirements and threats to their continued existence and alleviate those which threaten the species.

3. Develop and use an information/education program to solicit the assistance of local landowners, communities, and others to recover the species.

4. Search for additional populations, and through augmentation or reintroduction, establish viable populations.

5. Conduct anatomical and molecular genetic analysis of the species.

6. Develop and implement cryogenic preservation.

7. Develop and implement a monitoring program, and annually assess the recovery program where needed.

Date of Recovery: The downlisting and delisting dates cannot be estimated at this time. A time period of at least 10 years is needed to document the long-term viability of mussel populations.

Cost ($000s):

YEAR	NEED 1	NEED 2	NEED 3	NEED 4	NEED 5	NEED 6	NEED 7	TOTAL
2001	15.0	170.0	35.0	20.0	15.0	0.0	10.5	**265.5**
2002	15.0	170.0	25.0	45.0	20.0	25.0	10.5	**310.5**
2003	15.0	190.0	25.0	45.0	20.0	25.0	10.5	**330.5**
2004	15.0	160.0	20.0	45.0	20.0	25.0	10.5	**295.5**
2005	15.0	140.0	20.0	20.0	0.0	5.0	10.5	**210.5**
2006	15.0	140.0	20.0	20.0	0.0	5.0	10.5	**210.5**
2007	15.0	140.0	20.0	20.0	0.0	5.0	10.5	**210.5**
2008	15.0	140.0	20.0	20.0	0.0	5.0	10.5	**210.5**
2009	15.0	140.0	20.0	20.0	0.0	5.0	10.5	**210.5**
2010	15.0	140.0	20.0	20.0	0.0	5.0	10.5	**210.5**
2011	15.0	140.0	20.0	20.0	0.0	5.0	10.5	**210.5**
TOTAL	**165.0**	**1,670.0**	**245.0**	**295.0**	**75.0**	**110.0**	**115.5**	**2,675.5**

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PART I

INTRODUCTION

The Cumberland elktoe (*Alasmidonta atropurpurea* [Rafinesque 1831]), oyster mussel (*Epioblasma capsaeformis* [Lea 1834]), Cumberlandian combshell (*Epioblasma brevidens* [Lea 1831]), purple bean (*Villosa perpurpurea* [Lea 1861]), and rough rabbitsfoot (*Quadrula cylindrica strigillata* [Wright 1898]), were federally listed as endangered species under the Endangered Species Act of 1973, as amended (Act), on January 10, 1997 (Service 1997). These five freshwater mussels, all members of the family Unionidae, are endemic to either the Cumberland River system (Cumberland elktoe), the Tennessee River system (purple bean and rough rabbitsfoot), or to both river systems (oyster mussel and Cumberlandian combshell) (Figure 1). They have all undergone significant reductions in total range and population density. Having once existed in hundreds of river miles, they now survive in only a few relatively small, isolated populations of questionable long-term viability. The Cumberland elktoe still exists in 12 mostly small tributaries to the upper Cumberland River system in Kentucky and Tennessee. The oyster mussel survives in six tributaries of the Tennessee and Cumberland River systems in Kentucky, Tennessee, and Virginia. The Cumberlandian combshell persists in five tributaries of the Cumberland and Tennessee River systems in Alabama, Kentucky, Tennessee, Virginia, and Mississippi. The purple bean is extant in five tributaries and the rough rabbitsfoot is extant in three tributaries of the upper Tennessee River system in Tennessee and Virginia. These five species were eliminated from much of their historical ranges by anthropogenic factors, such as impoundments (not as significant a factor for the Cumberland elktoe and purple bean), channelization, pollution, sedimentation, and other significant factors. The species and their habitats are currently being impacted by deteriorated water and substrate quality (primarily resulting from poor land-use practices), contaminants, and, potentially, the invasion of the nonnative zebra mussel (*Dreissena polymorpha* [Pallas 1773]). Their restricted ranges and low population levels also increase their vulnerability to toxic chemical spills and the deleterious effects of genetic isolation. This agency draft recovery plan outlines the recovery objectives and criteria for the endangered Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot and the tasks needed to conserve and recover the species so they no longer require the protection afforded by the Act.

BACKGROUND

The North American mussel fauna includes at least 304 taxa (Turgeon et al. 1998) and represents the greatest diversity in the world (Williams and Neves 1995). More than 90 percent of the species inhabit the Southeastern United States (Neves et al. 1997). The Cumberlandian Region (Figure 1), with 37 percent of the fauna, is the primary center for North American freshwater mussel biodiversity (Ortmann 1918, 1925) and is one of six regional faunas on the continent (van der Schalie and van der Schalie 1950). The Cumberlandian Region (Figure 1) is defined as the Cumberland River and its tributaries downstream to the vicinity of Clarksville, Montgomery County, Tennessee; the Tennessee River and its tributaries downstream to the vicinity of Muscle Shoals, Colbert and Lauderdale Counties, Alabama; the Duck River (Tennessee River system) downstream to just below Columbia, Maury County, Tennessee (Ortmann 1924a); and the Buffalo River (a lower Duck River tributary) (van der Schalie 1973).

Historically, 95 mussel taxa (including 4 endemic and 25 Cumberlandian endemic) were found in the Cumberland River system (Gordon and Layzer 1989, Gordon 1995, Parmalee and Bogan 1998), while the Tennessee River system harbored 104 taxa (including 9 endemic and 31 Cumberlandian endemic) (Starnes and Bogan 1988, Cicerello et al. 1991, Parmalee and Bogan 1998). Collectively, 111 taxa historically inhabited the two river systems, and 35 taxa are endemic to the region (Starnes and Bogan

1988, Gordon and Layzer 1989, Cicerello et al. 1991, Gordon 1995, Parmalee and Bogan 1998).

There is evidence that mussel populations throughout the Central and Eastern United States remained relatively unchanged for centuries prior to European settlement, despite the consumption and use by Native Americans of huge numbers of mussels from numerous regional streams (Parmalee et al. 1982, Hughes and Parmalee 1999). Archeological evidence, however, suggests that the decline of Cumberlandian Region mussel populations began taking place before early researchers documented the historical fauna (Hughes and Parmalee 1999). Modern civilization began, by the late 1800s, to exploit mussel resources for pearls, as did Native Americans (Kunz 1898, Kunz and Stevenson 1908, Myer 1914, Anthony and Downing 2001); buttons (Lefevre and Curtis 1912, Anthony and Downing 2001); and even fish bait, hog feed, and occasionally human consumption (Davis 2000). Although simple mussel exploitation proved locally destructive, it was the significant alteration of aquatic habitats that fostered the early collapse of our native mussel resources on a grand scale (Higgins 1858; Lewis 1868; Kunz 1898; Kunz and Stevenson 1908; Ortmann 1909, 1918, 1924b, 1925; van der Schalie 1938, 1973; Hughes and Parmalee 1999).

No other wide-ranging faunal group in North America has experienced, or is undergoing, as profound a degree of imperilment as are the freshwater mussels (Stein and Flack 1997, Abell et al. 2000). An assessment of the continent's entire mussel fauna recommended conservation status for 67 percent (Stein and Flack 1997) to 72 percent (Williams et al. 1993, Williams and Neves 1995) of the taxa. As many as 36 taxa (13 percent) are presumed extinct (Howells et al. 1997, Neves et al. 1997, Neves 1999a), and 69 taxa (21 percent) are classified as federally endangered or threatened species, with some of these latter species considered extinct (Neves 1999a). Over one-third of the continent's mussel fauna either became extinct or was federally listed during the past century. The primary causes of this decline are loss of suitable habitat caused by impoundments, channelization, pollution, sedimentation, and other factors (Ortmann 1909, Fuller 1974, Williams et al. 1993, Williams and Neves 1995).

The general trend of increasing mussel imperilment has been documented at the global scale (Bogan 1993, Kay 1995). Experts have reluctantly resigned themselves to the fact that numerous additional taxa are "circling the drain"; these taxa are functionally extinct and/or are expected to become extinct in the foreseeable future (Neves 1993, 1997; Shannon et al. 1993; Ricciardi et al. 1998). Nott et al. (1995) noted that North American mussels and fishes have suffered recent extinction rates in the "kilo-death" range, or three orders of magnitude higher than the rates that have been estimated for species over geological time. They predict a major increase in the global extinction rate in the near future for freshwater mussels and other mollusks compared with the past global extinction rate.

The level of imperilment in the Southeastern mussel fauna (75 percent) exceeds that of the continent as a whole (Neves et al. 1997). Further focus of the Southeastern faunal imperilment indicates Tennessee River system mussels appear to have been the most severely impacted (Neves et al. 1997). There are far more mussel and fish species at risk (104) in the Cumberland and Tennessee River systems (including six of The Nature Conservancy's [TNC] top seven ranked small watershed areas for aquatic biodiversity) than in any other region in the country (Master et al. 1998). Other compilations of Cumberlandian Region species at risk recorded 68 mussel taxa, including all of the regional endemics (Williams et al. 1993), and 58 fish taxa (Warren et al. 2000). One-third (or 12 taxa) of all North American mussel species thought to be extinct were once known from, and primarily endemic to, the Cumberlandian Region. Even in the upper Clinch River system, which remains the crown jewel of current imperiled mussel populations in the Cumberlandian Region, the fauna has been slowly declining over the past century (Hampson 2000).

SPECIES DESCRIPTIONS

Cumberland elktoe

The Cumberland elktoe has a thin, but not fragile, shell. The outside surface of the shell (periostracum) is smooth, somewhat shiny, and covered with greenish rays. Young specimens have a yellowish brown periostracum, while specimens of adults are generally much darker. The inside surface of the shell (nacre) is shiny, with the color being white, bluish white, or sometimes peach or salmon. See Clarke (1981) and Parmalee and Bogan (1998) for a more complete description of the species and Parmalee and Bogan (1998) for a synonymy (history of name changes) of the species.

Gordon (1991) presents the following diagnostic characters to separate the Cumberland elktoe from the elktoe (*Alasmidonta marginata* [Say 1818]):

> This species is quite similar to *Alasmidonta marginata*, but tends to differ from the latter by its darker color, less pronounced corrugations on the posterior slope, and the less acutely angular development of the posterior ridge. In older individuals of *A. atropurpurea*, the posterior ridge may be rather high and the resulting slope may be quite steep, but the posterior ridge retains a rounded character. The two species may occur in adjacent stream systems but do not appear to be sympatric at any locality.

Oyster mussel

The oyster mussel has a periostracum that is dull to sub-shiny yellowish to green in color, with numerous narrow dark green rays. The shells of females are expanded along the posterior ventral margin and quite thin and fragile toward the shell's posterior margin. The nacre is whitish to bluish white in color. See Johnson (1978) and Parmalee and Bogan (1998) for a more complete description of the species and Parmalee and Bogan (1998) for a synonymy of the species.

Gordon (1991) provides the following diagnostic characters:

> The pronounced development of the posterior-ventral region in females distinguishes *Epioblasma* from similarly shaped species. [*Epioblasma*] *capsaeformis* is recognized by the typically dark coloration and fragility of the marsupial expansion and the lack of development of the posterior ridge (e.g., not angular, no knobs). Males in comparison to similar *Epioblasma* tend to be more elliptical, have a moderately developed posterior ridge and accompanying sulcus, and have a regularly curved ventral margin. The ventral margin in species such as E. [*f.*] *florentina* (Lea 1857) and *E. turgidula* (Lea 1858) often exhibit [sic] an emargination of the ventrum just anterior to the terminus of the posterior ridge. Yellowish specimens of *E. capsaeformis* have been mistaken for E. [*florentina*] walkeri (Wilson and Clarke 1914) (including records in Johnson [1978: as E. [*f.*] *florentina*). Males of *E.* [*florentina*] *walkeri* tend to be broader and have a rounded posterior ridge; females lack the distinctive darkening of the marsupial expansion.

Ortmann (1924a) was the first to note color differences in female oyster mussel mantle pads, which is presumably a host fish attractant. The mantle color appears to be bluish or greenish white in the Clinch River, greyish to blackish in the Duck River, and nearly white in the Big South Fork population (Ortmann 1924a, S. A. Ahlstedt and J. B. Layzer, U.S. Geological Survey [USGS], personal communication [pers. comm.], 1997). In addition, the Duck River form achieves nearly twice the size of other populations. Varying mantle coloration and, secondarily, size differential may be indications that more than one species is possibly represented within *Epioblasma capsaeformis* (see "Narrative Outline," Recovery Task 1.3.7).

Cumberlandian combshell

The Cumberlandian combshell has a thick solid shell with a smooth to clothlike periostracum, which is yellow to tawny brown in color with narrow green broken rays. The nacre is white. The shells of females are inflated, with serrated teethlike structures along a portion of the shell margin. See Johnson (1978) and Parmalee and Bogan (1998) for a more complete description of the species and Parmalee and Bogan (1998) for a synonymy of the species.

Gordon (1991) provides the following diagnostic characters:

> The broad, yellowish shell with broken rays and the distinctive marsupial expansion of the female distinguish this species from most other mussels in the range except *Pychobranchus fasciolaris* [(Rafinesque 1820)] and *Epioblasma lenoir* (Lea 1842). Male *E. brevidens* are broader than *P. fasciolaris* and the females of the latter species do not exhibit the marsupial development of the former. Raying patterns on *P. fasciolaris* usually are not developed. *Epioblasma lenoir* is a considerably smaller species, has a much lighter shell, tends to be greenish, does not have as developed a marsupial expansion, and probably is extinct.

Purple bean

The purple bean has a small to medium-sized shell. The periostracum is usually dark brown to black with numerous closely spaced fine green rays. The nacre is purple, but the purple may fade to white in dead specimens. See Bogan and Parmalee (1983) and Parmalee and Bogan (1998) for a more complete description of the species and Parmalee and Bogan (1998) for a synonymy of the species.

Gordon (1991) provides the following diagnostic characters:

> *Villosa perpurpurea* most closely resembles *V. trabalis* [(Conrad 1834)]. The most obvious difference is the purple nacre of the former in comparison to the white nacre of the latter. However, this character is somewhat variable as noted by Ortmann (1925) and the purple color may fade rapidly in dead specimens. With regards to other shell characters, [*V.*] *perpurpurea* tends to be more compressed, thinner, slightly broader, the beak is less developed, and the emargination of the ventral margin in female shells is not as pronounced. The base color of the periostracum in [*V.*] *trabalis* is greenish. Simpson (1914) noted that *perpurpurea* was "less exaggerated in its particular characters than [*V.*] *trabalis*." The

> glochidia of the two species are also shaped differently (Hoggarth, 1988). *Villosa vanuxemii* [=*V. v. vanuxemensis*] (Lea 1838) may be sympatric with *perpurpurea* but it tends to be a bit larger. Its [*V. vanuxemii*] nacre is shiny purple but tends to be reddish or brownish in the area of the beak cavity and may be lighter around the periphery of the shell, the base color of the periostracum is brown, and raying is rather obscure. Female shells are strongly truncated, often with a distinct notch just ventral to the terminus of the posterior ridge which runs approximately parallel to the dorsal margin.

Rough rabbitsfoot

The rough rabbitsfoot has an elongated, heavy, highly pustulate (bumpy) shell. Some specimens may have low knobs on the posterior slope. The periostracum is yellowish to greenish in color and is covered with green rays, blotches, and chevron patterns. The nacre is silvery to white with iridescence in the posterior area of the shell. See Bogan and Parmalee (1983) and Parmalee and Bogan (1998) for a more complete description of the species and Parmalee and Bogan (1998) for a synonymy of the species.

Gordon (1991) provides the following diagnostic characters:

> The tendency for the shell to be compressed, highly pustulate, and have low to no knobs on the posterior ridge distinguishes this morph from *Quadrula cylindrica* s. s. [i.e., *Q. c. cylindrica* (Say 1817)]. It is not easily confused with any other sympatric species . . . .

DISTRIBUTIONAL HISTORY AND RELATIVE ABUNDANCE

General Information

The Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot are all endemic to either the Cumberland River system (Cumberland elktoe), the Tennessee River system (purple bean and rough rabbitsfoot), or to both these river systems (oyster mussel and Cumberlandian combshell) (Figure 1). Once widespread in the Cumberlandian Region, these species' ranges are currently highly fragmented, and most of their populations are of questionable viability long-term.

The downstream extent of the Cumberlandian Region approximately coincides with the westernmost portion of the Highland Rim Physiographic Province, near the Coastal Plain Physiographic Province (Mississippi embayment). The gradient of the Cumberland and Tennessee Rivers downstream of this area decreases to the extent that the shoal habitat upon which Cumberlandian mussel species depend was historically extremely scarce or nonexistent. Most of the larger river reaches at the western edge of the Highland Rim are now impounded by the Barkley (Cumberland River) and Kentucky (Tennessee River) Reservoirs.

The mussel fauna of the Cumberlandian Region has been the subject of numerous zoogeographic studies since the work of Lewis (1870) on the Tennessee River at Knoxville. Extensive survey information has become available since 1960 (see Gordon and Layzer [1989] and Winston and Neves [1997] for stream-specific survey citations). These faunal studies form the basis upon which the distributional history of the species addressed in this recovery plan are outlined (Tables 1 through 5).

Distributional History and Relative Abundance of the Five Species

In compiling the vast amount of distributional information on the five species in this section, numerous details should be clarified for the reader. Footnotes have been used liberally in Tables 1 through 5 in an effort to clarify erroneous, ambiguous, or otherwise complex records in these species' long distributional histories. Note that the authority for a particular occurrence is not necessarily exclusive but that the same occurrence may have been noted by multiple authorities. Personal communications with mussel researchers active in the Cumberlandian Region have served as the authority for more recent records of these species. Compilation studies (e.g., Johnson 1978, Bogan and Parmalee 1983, Schuster 1988, Gordon 1991) are given as an authority only when no primary authority can be identified or no significant additional dates of collection can be verified. Schuster (1988) and Gordon (1991) records were compiled from the following museums: Academy of Natural Sciences, Philadelphia; Carnegie Museum; Ohio State University Museum of Zoology; University of Michigan Museum of Zoology; and U.S. National Museum. Schuster (1988) also reported records from the Museum of Comparative Zoology.

Records in Tables 1 through 5 are for live or fresh dead shell material unless specimens were considered to be relic or of archeological age or origin. Relic shells had nacre that lacked the luster of fresh dead specimens and had been considered dead for at least several months, if not years or decades. Archeological records represent specimens collected from archeological sites or specimens that are subfossil in appearance (e.g., flaky periostracum, chalky nacre, brittle shell); such material is generally construed as having been dead for centuries. In general, 1985 represented the rather arbitrary cutoff date for determining whether a species was considered extant or extirpated from a stream, unless more recently available information indicated otherwise. Exceptions to these assumptions are to be expected with further survey data. Common and scientific names follow Turgeon et al. (1998).

Cumberland elktoe

The Cumberland elktoe is limited in distribution to the upper Cumberland River system in southeast Kentucky and north-central Tennessee, occupying streams both above and below Cumberland Falls (Table 1). This species appears to have occurred only in the main stem of the Cumberland River and primarily its southern tributaries upstream from the hypothesized original location of Cumberland Falls near Burnside, Pulaski County, Kentucky (Cicerello and Laudermilk 2001). The original type locality was simply "river Cumberland," according to Clarke (1981), who, upon ascertaining that the type specimen was lost, designated a neotype from the Clear Fork River, a tributary to the Big South Fork, in Fentress County, Tennessee (see Table 1, Footnote 2). All verified sites of occurrence are in the Cumberland Plateau Physiographic Province, giving it one of the most restricted ranges of any Cumberlandian species.

There has been confusion about the historical distribution of this species because of its similarity to a congener--the elktoe (*Alasmidonta marginata*) (Cicerello and Laudermilk 2001). Museum and literature records of *A. marginata* from the Cumberland River drainage on the Cumberland Plateau should be verified because they may actually represent the Cumberland elktoe (see note for Table 1). Cicerello and Laudermilk (2001) maintains that these two species occur sympatrically in the Rockcastle River, contrary to the assertion by Gordon and Layzer (1993) that they are allopatric.

The Cumberland elktoe has apparently been extirpated from the main stem of the Cumberland River and Laurel River and its tributary, Lynn Camp Creek. The status of the Cumberland elktoe from the heavily coal-mined New River watershed, where there is a single known record (Gordon 1991), is unknown. Based on recent records, populations of the Cumberland elktoe persist in 12 tributaries--Laurel Fork, Claiborne County, Tennessee and Whitley County, Kentucky and Marsh Creek, McCreary County, Kentucky ; Sinking Creek, Laurel County, Kentucky; Big South Fork, Scott County, Tennessee, and McCreary County, Kentucky; Rock Creek, McCreary County, Kentucky; North White Oak Creek, Fentress County, Tennessee; Clear Fork, Fentress, Morgan, and Scott Counties, Tennessee; North Prong Clear Fork and Crooked Creek, Fentress County, Tennessee; White Oak Creek, Scott County, Tennessee; Bone Camp Creek, Morgan County, Tennessee; and New River, Scott County, Tennessee (Table 1). The latter nine streams, which comprise the Big South Fork system, may represent a single metapopulation of the Cumberland elktoe; there may be suitable habitat for the species and/or its fish hosts in intervening stream reaches, potentially allowing for natural genetic interchange to occur.

Considered a “rare species” by Clarke (1981), few sites continue to harbor the Cumberland elktoe. Marsh Creek harbors the largest population known in Kentucky (Cicerello 1995), and the population in Rock Creek is also sizable (Cicerello 1996). In both streams the Cumberland elktoe represented the second most abundant unionid species (Cicerello 1995, 1996). The Marsh Creek population, with at least three year classes present, is viable, but the viability of the Rock Creek population is questionable (R. R. Cicerello, Kentucky State Nature Preserves Commission, pers. comm., 2000). The largest population in Tennessee is in the Big South Fork system in the headwaters of the Clear Fork system, where several hundred specimens were found in muskrat middens in the late 1980s (Bakaletz 1991; Layzer, pers. comm., 1998). Several age classes of the Cumberland elktoe were represented in samples taken from throughout the larger tributaries of the Big South Fork system in Tennessee during a 1985-86 survey (Bakaletz 1991).

Oyster mussel

The oyster mussel was described from the Cumberland River, Tennessee, possibly from Davidson County (Nashville), and historically was one of the most widely distributed Cumberlandian mussel species (Table 2). Its range historically included four physiographic provinces (i.e., Interior Low Plateau, Cumberland Plateau, Ridge and Valley, Blue Ridge) and six States (i.e., Alabama, Georgia, Kentucky, North Carolina, Tennessee, Virginia). In the Cumberland River it occurred from the base of Cumberland Falls, McCreary and Whitley Counties, Kentucky, downstream to Stewart County, Tennessee. In the Tennessee River it occurred throughout the main stem downstream to Colbert and Lauderdale Counties, Alabama. Dozens of tributaries in the Cumberland and Tennessee River systems also harbored this species. The most downstream site known from the Cumberland River represents an archeological record (P. W. Parmalee, McClung Museum, University of Tennessee, pers. comm., 1997), indicating that at least in premodern times this species occurred further downstream from the area strictly defined as the Cumberlandian Region.

Many streams no longer harbor populations of the oyster mussel. Populations have been totally eliminated from both main stems of the Cumberland and Tennessee Rivers (Table 2). In addition, populations have apparently been extirpated from most tributaries of the Cumberland River system (e.g., Rockcastle River, Beaver Creek, Obey River, Caney Fork, Harpeth River) and the Tennessee River system (e.g., Little River [in Virginia], Wallen Creek, Poplar Creek, North Fork Holston River, Big Moccasin Creek, South Fork Holston River, Holston River, French Broad River, Little Pigeon River, West Prong Little Pigeon River, Little River [in Tennessee], Little Tennessee River, Hiwassee River, South Chickamauga Creek, Lookout Creek, Sequatchie River, Paint Rock River, Estill Fork, Larkin Fork, Hurricane Creek, Flint River, Limestone Creek, Elk River, Richland Creek, Shoal Creek, Bear Creek, Buffalo River). The oyster mussel has also been extirpated from large portions of additional Cumberlandian streams (e.g., Clinch and Duck Rivers), from the entire Blue Ridge Physiographic Province, and is apparently no longer found in the States of Alabama (*contra* Lydeard et al. 1999), Georgia, and North Carolina (Table 2).

In the Cumberland River system, oyster mussel populations remain in isolated stretches of the Big South Fork, Scott County, Tennessee, and McCreary County, Kentucky. (However, there is conjecture as to the true identity of these specimens; they might actually represent *Epioblasma florentina walkeri* [see Table 2, Footnote 1] or an undescribed species [Ahlstedt, pers. comm., 2002]. Molecular genetic studies of this form are needed to solve this issue [see Task 1.3.7]. If they are indeed *E. florentina walkeri*, the oyster mussel is probably extirpated from the entire Cumberland River system). Although a 1984 record exists for Buck Creek, Pulaski County, Kentucky

(Table 2), a recent resurvey of the stream failed to produce even a relic shell (Hagman 2000). The oyster mussel is probably now extirpated from Buck Creek. Recent Tennessee River system records include the Clinch River, Russell and Scott Counties, Virginia, and Hancock County, Tennessee; Powell River, Lee County, Virginia; North Fork Holston River, Scott County, Virginia (reintroduced population); Nolichucky River, Cocke and Hamblen Counties, Tennessee; and Duck River, Marshall County, Tennessee (Table 2). Although reported from Copper Creek in 1991 and 1995 (Ahlstedt, pers. comm., 1997), survey efforts in 1998 failed to find even a relic shell of the oyster mussel (Fraley and Ahlstedt 2001). They thought the oyster mussel "may be extirpated" from this stream, but the species is considered possibly still extant in Copper Creek in this recovery plan.

Historically, the oyster mussel appears to have been widespread and common in the Cumberlandian Region, especially in the Tennessee River system (Johnson 1978). Wilson and Clark (1914) stated that it was "fairly common" in the Big South Fork, but that it was found "sparingly" in the main stem of the Cumberland River. Neel and Allen (1964) found it to be rare to abundant in the main stem of the Cumberland River. It was reported as being abundant throughout the Tennessee River system, particularly in the upper portion (Ortmann 1918, 1925).

A quantitative study by Ahlstedt and Tuberville (1997) in the Powell and Clinch Rivers in Tennessee and Virginia provides insight into recent oyster mussel densities in the upper Tennessee River system. Sampling at 14 to 16 sites (varied by year) in the Powell River revealed the oyster mussel to "occur in extremely low densities," and it was found during only the first 2 of the 4 years of sampling effort. Taking at least 432 quadrats (2.7 square feet) per year, they were found at densities of 0.76 and 0.22 per square foot in 1979 and 1983, respectively, but they were absent from the 1988 and 1994 samples. Limited quantitative sampling for the oyster mussel in the Powell River in Virginia by Wolcott and Neves (1994) during 1988 and 1989 revealed no specimens. Similar sampling at

11 to 14 sites in the Clinch River revealed the oyster mussel at considerably higher densities than in the Powell River in 2 of the 3 years represented (Ahlstedt and Tuberville 1997). Sampling at least 345 quadrats per year, they found densities of 3.24, 0.11, and 2.92 per square foot in 1979, 1988, and 1994, respectively. According to Ahlstedt and Tuberville (1997), a prolonged drought between 1983 and 1988 probably accounted for the low numbers during the sampling efforts expended in 1988 (see comments on coal mining in "Past and Present Threats").

Neves (1991) considered the oyster mussel to be "extremely rare" throughout the upper Tennessee River system, an observation based partially on the work of Dennis (1987) that documented the recent decline of this once abundant species in the Clinch River. During 1996 and 1997, however, biologists documented evidence of recent recruitment of the oyster mussel at certain localities in the Clinch River in both Virginia (L. M. Koch, Service, pers. comm., 1997) and Tennessee (Ahlstedt, pers. comm., 1997). The Duck River also apparently harbors a fairly healthy population of this species (J. T. Garner, Alabama Division of Wildlife and Freshwater Fisheries, pers. comm., 1997). The Big South Fork oyster mussel population, which may represent the only viable population in the entire Cumberland River system, is small (Bakaletz 1991) compared to those extant populations in the Clinch and Duck Rivers.

Cumberlandian combshell

The Cumberlandian combshell was described from the Cumberland River in Tennessee, possibly from Davidson County (Nashville). Historically, it ranged throughout the Cumberlandian Region (Table 3), occurring in three physiographic provinces (i.e., Interior Low Plateau, Cumberland Plateau, Ridge and Valley) and five states (i.e., Alabama, Kentucky, Mississippi, Tennessee, Virginia). In the Cumberland River it occurred from the base of Cumberland Falls, McCreary and Whitley Counties, Kentucky, downstream to Stewart County, Tennessee. In the Tennessee River, it occurred throughout the main stem downstream to Benton and Humphreys Counties, Tennessee. The Cumberlandian combshell also occurred in numerous tributaries in the Cumberland and Tennessee River systems. The most downstream records in both rivers are from archeological sites (Parmalee and Bogan 1998), indicating that at least in premodern times this species occurred further downstream from the area strictly defined as the Cumberlandian Region.

The Cumberlandian combshell has been extirpated from a large percentage of its former range (Table 3). Main-stem Tennessee River populations are no longer found. If extant, only senescent individuals comprise the Cumberland River main-stem population known circa 1980 from the Tennessee portion of that river (Parmalee et al. 1980, Gordon 1991). This species has apparently also been eliminated from numerous tributaries in the Cumberland (e.g., Rockcastle River, Beaver Creek, Obey River, Caney Fork, Stones River, Red River) and Tennessee (e.g., Station Creek, Wallen Creek, Holston River, Nolichucky River, West Prong Little Pigeon River, Little Tennessee River, Paint Rock River, Elk River, Little Bear Creek, Cedar Creek, Duck River) River systems (Table 3). The Cumberlandian combshell has also been extirpated from large portions of additional tributaries in the Cumberlandian Region (e.g., Clinch River, Powell River, North Fork Holston River, Bear Creek).

Extant Cumberland River system populations occur in Buck Creek, Pulaski County, Kentucky; and Big South Fork, Scott County, Tennessee, and McCreary County, Kentucky (Table 3). In the Tennessee River system, populations are thought to remain in the Powell River, Lee County, Virginia, and Claiborne and Hancock Counties, Tennessee; Clinch River, Scott County, Virginia, and Hancock County, Tennessee; North Fork Holston River, Scott County, Virginia (reintroduced population); and Bear Creek, Colbert County, Alabama and Tishimingo County, Mississippi (Table 3).

Historically, the Cumberlandian combshell appears to have been widespread and common at many sites in larger Cumberlandian Region streams. Neel and Allen (1964) reported it as being "very common" in the upper Cumberland River below Cumberland Falls in the late 1940s. Ortmann (1924a, 1925) reported it as relatively abundant in the upper Tennessee River system but rare in the lower Tennessee and Cumberland River systems.

Recent density information is available for the Cumberlandian combshell in the headwaters of the Tennessee River system. Ahlstedt and Tuberville (1997) quantitatively assessed populations since 1979 in the Powell and Clinch Rivers, Tennessee and Virginia. Sampling at 14 to 16 sites (varied by year) in the Powell River revealed the Cumberlandian combshell to be "rare" over the course of the 15-year study. Taking at least 432 quadrats (2.7 square feet) per year, they recorded a steady decline in densities of 0.97, 0.54, 0.32, and 0.11 per square foot in 1979, 1983, 1988, and 1994, respectively. Similar sampling at 11 to 14 sites in the Clinch River revealed a gradual increase in Cumberlandian combshell densities of 0.32, 0.65, and 0.76 per square foot in 1979, 1988, and 1994, respectively, from the minimum of 345 quadrats taken each year (Ahlstedt and Tuberville 1997). They attributed the decline in Powell River populations of this species to general stream degradation (see comments on coal mining in "Past and Present Threats"). Wolcott and Neves (1994) conducted both qualitative and limited quantitative sampling for mussels in the Powell River in Virginia during 1988 and 1989. Two of the five sites that qualitatively yielded Cumberlandian combshell specimens had densities of 0.03 and 0.01 per square foot, respectively.

The Cumberlandian combshell was considered "extremely rare" by the 1980s throughout its range, and its numbers were declining in the upper Tennessee River system, particularly in Virginia (Neves 1991, Dennis 1987). Currently, the largest extant population of the Cumberlandian combshell probably occurs in the Clinch River in Virginia and Tennessee (Ahlstedt, pers. comm., 1998). Biologists have recently documented the presence of significant numbers of adults and verified recent recruitment with the presence of juvenile specimens from muskrat middens in the Clinch River (Ahlstedt and Koch, pers. comm., 1997). Populations in other stream reaches are small (e.g., Buck Creek, Big South Fork, Powell River, Duck River) (Bakaletz 1991, Wolcott and Neves 1994, Hagman 2000; Ahlstedt, pers. comm., 1997).

Purple bean

The purple bean is endemic to the upper Tennessee River system above its confluence with the Clinch River (Table 4). Its type locality was stated simply as "Tennessee"; therefore, the type locality is not included in Table 4. Primarily a species of the Ridge and Valley Physiographic Province, it also occurs at the eastern edge of the Cumberland Plateau. The entire range of the purple bean occurs in northeastern Tennessee and southwestern Virginia.

The purple bean has apparently been extirpated from the Powell River, North Fork Holston River, Emory River, and North Fork Beech Creek (Table 4). Extant populations are located in isolated portions of the Clinch River, Tazewell, Russell, and Scott Counties, Virginia; Indian Creek, Tazewell County, Virginia; Copper Creek, Scott County, Virginia; Obed River, Cumberland County, Tennessee; and Beech Creek, Hawkins County, Tennessee (Table 4).

Ortmann (1918) considered the purple bean as being "not rare" in the Virginia portion of the Clinch River. A recent quantitative study by Ahlstedt and Tuberville (1997) in the Clinch River in Tennessee and Virginia revealed this species to be "rare" over the 15-year sampling period. Periodic sampling (approximately 4-year intervals) of at least 345 quadrats from 11 to 14 sites in the Clinch revealed densities of 0.11 per square foot in both 1979 and 1988, but no specimens were taken during 1994. Neves (1991) reported that it was uncommon to rare throughout its range and that populations were declining.

Currently, population sizes are all generally small. The largest population may have occurred in the upper Clinch River/Indian Creek (Ahlstedt, pers. comm., 1997) prior to a Clinch River chemical spill in late 1998 that resulted in the death of at least 52 specimens (see “Reasons for Decline”). Neves (1991) considered the Copper Creek population to be the largest, but that population has been decimated. Fraley and Ahlstedt (2001) found only two live specimens and a single fresh dead shell during their 1998 qualitative resurvey of Copper Creek (see Ahlstedt 1982). The status of the Emory River system population is tenuous. It remains at two sites in the Obed River but in very low numbers (Ahlstedt, pers. comm., 2001). The Beech Creek population, the only extant purple bean population in the Holston River system, is probably also declining (Ahlstedt, pers. comm., 2001). Recent qualitative survey work (February 2001) located 74 live specimens; most were found exposed on the substrate while apparently spawning (S. J. Fraley, Tennessee Valley Authority [TVA], unpublished data). Live individuals were located at 9 of 12 Beech Creek sites sampled, and some evidence of recent recruitment was observed. Beech Creek probably harbors the largest and healthiest remaining purple bean population rangewide, but it appears tenuous because riparian development and agricultural impacts were prevalent in the watershed (R. S. Butler, pers. obs., 2001).

Rough rabbitsfoot

The rough rabbitsfoot is considered a subspecies of the wide-ranging rabbitsfoot, *Quadrula c. cylindrica.* The type locality is the Clinch River in Virginia (erroneously given as “Lee Co., VA.”; Ortmann 1918). The historical distribution of this taxon is generally considered to be above Norris Reservoir (Powell and Clinch Rivers) and in the fork of the Holston River in northeastern Tennessee and southwestern Virginia (Ortmann 1918). Downstream (main stem of the Tennessee River and larger tributaries), the typical form (*Quadrula c. cylindrica*) is presumed to have occurred. The rough rabbitsfoot is restricted to the upland-most portion of the Ridge and Valley Physiographic Province, making it one of the more narrowly distributed species endemic to the Cumberlandian Region (Table 5).

Ortmann (1924a) stated that the range of the rough rabbitsfoot was the headwaters of the Powell, Clinch, and Holston Rivers. Today, the entire Holston River system population of the rough rabbitsfoot has been extirpated (e.g., North and South Fork Holston Rivers and Big Moccasin and Possum Creeks) (Table 5). Populations of this species remain in the Clinch River, Russell and Scott Counties, Virginia (and possibly Tazewell--see Table 5, Footnote 1), and Hancock County, Tennessee; Indian Creek, Tazewell County, Virginia; and Powell River, Lee County, Virginia, and Hancock and Claiborne Counties, Tennessee (Table 5). Although reported from Copper Creek in 1991 (Ahlstedt, pers. comm., 1997), only relic shells were reported in 1998 (Fraley and Ahlstedt 2001), indicating it "may be extirpated" from the stream. For the purpose of this recovery plan, the species is considered possibly still extant in Copper Creek.

Recent quantitative population density information is available for the rough rabbitsfoot in the Powell and Clinch Rivers in Tennessee and Virginia. Sampling by Ahlstedt and Tuberville (1997) revealed "extremely low densities" of the rough rabbitsfoot in the Powell, and a decline in the Clinch, over the course of the 15-year study. Taking at least 432 quadrats (2.7 square feet) at 14 to 16 sites per year, they found Powell River densities of 0.11 per square foot in both 1979 and 1988 but none in 1983 and 1994 samples. Similar sampling of at least 345 quadrats from 11 to 14 sites in the Clinch River revealed densities of 1.84 and 0.32 per square foot in 1979 and 1994, respectively. According to Ahlstedt and Tuberville (1997), a prolonged drought between 1983 and 1988 at least partially accounted for the low numbers detected during 1988 sampling efforts (see comments on coal mining in "Past and Present Threats"). Limited quantitative sampling in the Powell River in Virginia by Wolcott and Neves (1994) during 1988 and 1989 revealed no specimens of the rough rabbitsfoot.

Preimpoundment historical abundance of this species was not recorded by Ortmann (1918) or any other investigator. Current population size of the rough rabbitsfoot is largest in the Clinch River, in general, but particularly in the Scott County, Virginia, portion of the Clinch, where it may be locally abundant (Yeager and Neves 1986, Ahlstedt 1991a). Its population status elsewhere appears to be much more tenuous. Efforts by the TVA to transplant specimens into the North Fork Holston River during the mid-1970s (Ahlstedt 1980) have apparently failed (Ahlstedt, pers. comm., 1997).

HABITAT

General Information

Adult mussels are ideally found in localized patches (beds) in streams, almost completely burrowed in the substrate with only the area around the siphons exposed (Balfour and Smock 1995). The composition and abundance of mussels are directly linked to bed sediment distributions (Neves and Widlak 1987, Leff et al. 1990). Physical qualities of the sediment (e.g., texture, particle size) may be important in allowing the mussels to firmly burrow in the substrate (Lewis and Riebel 1984). These and other aspects of substrate composition, including bulk density (mass/volume), porosity (ratio of void space to volume), sediment sorting, and the percentage of fine sediment, may also influence mussel densities (Brim Box 1999, Brim Box and Mossa 1999). Water velocity may be a better predictor than substrate for determining where certain mussel species are found in streams (Huehner 1987). In general, heavy-shelled species occur in stream channels with currents, while thin-shelled species occur in more backwater areas.

Stream geomorphic and substrate stability is especially crucial for mussel species and for maintaining diverse, viable mussel beds (Vannote and Minshall 1982, Hartfield 1993, Di Maio and Corkum 1995). Where substrates are unstable, conditions are generally poor for mussel habitation. The most stable portion of a stream's bottom is oftentimes under slab boulders, an excellent microhabitat to search for numerous mussel species (Ahlstedt, pers. comm., 1999). See "Past and Present Threats" for a detailed discussion about how various activities cause channel instabilities that result in substrate conditions that are not conducive to mussels. Although several studies have related adult habitat selection with substrate composition, most species tend to be habitat generalists (Tevesz and McCall 1979, Strayer 1981, Hove and Neves 1994, Strayer and Ralley 1993), with few exceptions (Stansbery 1966).

Strayer (1999a) demonstrated in field trials that mussels in streams occur chiefly in flow refuges, or relatively stable areas that displayed little movement of particles during flood events. Flow refuges conceivably allow relatively immobile mussels to remain in the same general location throughout their entire lives. He thought that features commonly used in the past to explain the spatial patchiness of mussels (e.g., water depth, current speed, sediment grain size) were poor predictors of where mussels actually occur in streams.

Habitat and stream parameter preferences for juveniles are largely unknown (Neves and Widlak 1987). This is possibly due to a prevalent lack of evidence of recruitment, inadequate sampling methods, or reproductive failure (Coon et al. 1977; Strayer 1981; Moore 1995; McMurray et al. 1999a, 1999b). Isley (1911) stated that juveniles may prefer habitats that have sufficient oxygen, are frequented by fish, and are free of shifting sand and silt accumulation. Neves and Widlak (1987) suggested that juveniles inhabit depositional areas with low flow, where they can feed pedally (see "Food Habits") and siphon water from interstitial spaces among substrate particles (Yeager et al. 1994). Recent laboratory experiments determined that juvenile *Lampsilis fasciola* Rafinesque 1820 generally congregated in the top 0.8 inch of substrate (R. J. Neves, USGS, pers. comm., 2000). Juvenile mussels of certain species stabilize themselves by attaching to rocky and other substrates with a byssus (Frierson 1905, Isley 1911, Howard 1922).

Neves and Widlak (1987) summarized stream parameter preferences of habitat, substrate, current velocity, and presence of other bivalves for juvenile unionids. Initially, juveniles were clumped in runs and riffles, occurred primarily behind boulders, and were significantly correlated with the presence of the fingernail clam. They surmised that the habitat of older juveniles (i.e., ages 2 and 3 years) was similar to that of adults. Nevertheless, it remains unknown if juveniles of most species experience differential survival rates among different habitat parameters, if they remain in the habitat of the host fish, or if they exhibit any habitat preference (Neves and Widlak 1987).

Habitat of the Five Species

Cumberland elktoe

This species inhabits medium-sized rivers and may extend into headwater streams where it is often the only mussel present (Gordon and Layzer 1989, Gordon 1991). Gordon and Layzer (1989) reported that the species appears to be most abundant in flats, which were described by Gordon (1991) as shallow pool areas lacking the bottom contour development of typical pools, with sand and scattered cobble/boulder material, relatively shallow depths, and slow (almost imperceptible) currents. They also report the species from swifter currents and in areas with mud, sand, and gravel substrates.

Oyster mussel

This species inhabits small to medium-sized rivers (Dennis 1985), and sometimes large rivers, in areas with coarse sand to boulder substrate (rarely in mud) and moderate to swift currents (Gordon 1991). It is sometimes found associated with water-willow (*Justicia americana*) beds (Ortmann 1924a, Gordon and Layzer 1989) and in pockets of gravel between bedrock ledges in areas of swift current (Neves 1991). Gordon (1991) reports that this species, like other freshwater mussels, can bury itself below the substrate surface, but females have been observed to lie on top of the substrate while displaying and releasing glochidia.

Cumberlandian combshell

This species inhabits medium-sized streams to large rivers on shoals and riffles in coarse sand, gravel, cobble, and boulders (Dennis 1985, Gordon 1991). It is not associated with small stream habitats (Dennis 1985) and tends not to extend as far upstream in tributaries. In general, it occurs in larger tributaries than does its congener the oyster mussel. Gordon (1991) states that the species prefers depths less than 3 feet, but it appears to persist in the deep-water areas of Old Hickory Reservoir on the Cumberland River, where there is still fairly strong flow from the Cordell Hull and Center Hill Reservoirs (Gordon and Layzer 1989).

Purple bean

This species inhabits small headwater streams (Neves 1991) to medium-sized rivers (Gordon 1991). It is found in moderate to fast-flowing riffles with sand, gravel, and cobble substrates (Neves 1991) and rarely occurs in pools or slack water (Ahlstedt 1991a). It is sometimes found out of the main current adjacent to water-willow beds and under flat rocks (Ahlstedt 1991a, Gordon 1991).

Rough rabbitsfoot

This species inhabits medium-sized to large rivers in moderate to swift current but often exists in areas close to, but not in, the swiftest current (Gordon 1991). It is reported to live in silt, sand, gravel, or cobble in eddies at the edge of midstream currents and may be associated with macrophyte beds (Yeager and Neves 1986, Gordon 1991).

LIFE HISTORY

Food Habits

Adult freshwater mussels are filter feeders, orienting themselves in the substrate to facilitate the siphoning of the water column for oxygen and food (Kraemer 1979). Specific food habits of all five species are unknown, but they likely ingest food items similar to those consumed by other freshwater mussels. Mussels are known to consume detritus, diatoms, phytoplankton, zooplankton, and other microorganisms (Coker et al. 1921, Churchill and Lewis 1924, Fuller 1974). According to Ukeles (1971), phytoplankton is the principal food of bivalves. However, other food sources (e.g., bacteria, organic detritus, assimilated organic material, phagotrophic protozoans) may also play an important role (Neves et al. 1996). According to Baldwin and Newell (1991), bivalves feed on an entire array of naturally available particles (e.g., heterotrophic bacteria, phagotrophic protozoans, phytoplankton). Churchill (1916) concluded that mussels could absorb various sources of fat, protein, and starch dissolved in the water. Based on the findings of studies such as Baldwin and Newell (1991) and Neves et al. (1996), an omnivorous opportunistic diet would allow mussels to take advantage of whatever food type happens to be abundant. Gordon (1991) suggests that detritus may be an important food source for the Cumberland elktoe, which inhabits small headwater streams with little available plankton.

Juvenile mussels employ foot (pedal) feeding and are thus suspension/deposit feeders (Yeager et al. 1994). Video observations of *Villosa iris* (Lea 1829) by Yeager et al. (1994) revealed juveniles occupying the top 0.4 inch of sediment and employing the following two types of feeding mechanisms: (1) collecting organic and inorganic particles that adhere to the foot and conveying them to the pedal valve gape with sweeping motions and (2) extending the foot anteriorly, pulling themselves along while picking up organic and inorganic particles on the foot. These methods of suspension feeding have been termed pedal sweep feeding and pedal locomotory feeding, respectively (Reid et al. 1992). The juvenile diet (up to 2 weeks of age) includes bacteria, algae, and diatoms, with some detrital and inorganic colloidal particles (Yeager et al. 1994). In juvenile freshwater mussel feeding experiments, Neves et al. (1996) found that algae were suitable as food but that a tri-algal diet high in oils resulted in better growth. Silt provided some nutritional value, which was also observed by Hudson and Isom (1984), but bacteria in riverine sediment were not essential to growth and survival (Neves et al. 1996).

Growth and Longevity

Growth rates for freshwater mussels tend to be relatively rapid for the first few years (Chamberlain 1931, Scruggs 1960, Negus 1966) then slow appreciably (Bruenderman and Neves 1993, Hove and Neves 1994). The relatively abrupt slowing in growth rate occurs at sexual maturity, probably as a result of energy being diverted from growth to gamete production. Growth rates vary among species; heavy-shelled species grow slowly relative to thin-shelled species (Coon et al. 1977, Hove and Neves 1994). Under shoal habitat conditions (where high water velocities in river shallows are characterized by increased oxygen levels and food availability per unit time), growth rates are probably higher (Bruenderman and Neves 1993). This appears to be true for the Cumberlandian combshell in the Big South Fork (Ahlstedt, pers. comm., 2000).

As a group, mussels are extremely long-lived, with maximum life spans of 100 to 200 years for certain species (Neves and Moyer 1988, Bauer 1992, Mutvei et al. 1994). Heavy-shelled species, which includes many riverine forms, tend to reach higher maximum ages (Stansbery 1961). No age-specific information is available for these five species. However, considering the longevity of thick-shelled species (Stansbery 1961) such as the rough rabbitsfoot, it would seem probable that this species has a fairly long life span.

General Reproductive Biology of Mussels

Following is a summary of freshwater mussel reproduction (see Watters [1994] for an annotated bibliography of mussel reproduction). Freshwater mussels generally have separate sexes, although hermaphroditism is known for some species (van der Schalie 1970, Bauer 1987, Downing et al. 1989). Bauer (1987) conducted an experiment with the eastern pearlshell, *Margaritifera margaritifera* (Linnaeus 1758), which determined that some specimens (mostly females) changed sex to hermaphrodites when moved from dense populations to unpopulated areas. He concluded that hermaphroditism may be rare in dense mussel populations but more prevalent in sparse populations, perhaps as an adaptive response to a paucity or lack of sexual counterparts. If true, this phenomenon may help explain why perpetually sparse populations of certain extremely rare species have been known to persist for decades (Neves, pers. comm., 1997).

The age of sexual maturity for mussels is variable, usually requiring from 3 years (Zale and Neves 1982) to 9 years (Smith 1979), and may be sex dependent (Smith 1979). Males expel clouds of sperm into the water column, although some species expel spermatozeugmata (sperm balls), which consist of thousands of sperm (Barnhart and Roberts 1997). Females draw in sperm with the incurrent water flow. Fertilization takes place in their suprabranchial chambers, and the resulting zygotes develop into specialized veliger larvae, termed “glochidia,” in water tubes of the gills.

Three subfamilies are generally recognized within the family Unionidae (Parmalee and Bogan 1998)--Unioninae (or Ambleminae) (e.g., *Quadrula*, *Pleurobema*); Anodontinae (e.g., *Alasmidonta*, *Pyganodon*); and Lampsilinae (e.g., *Epioblasma*, *Villosa*). Depending on the subfamily, all four gills or just the outer gills (Unioninae), the entire outer pair of gills (Anodontinae, some Unioninae), or discreet portions of the outer pair of gills (Lampsilinae) are used as marsupia, or brood chambers, for glochidia. However, Heard and Guckert (1970) argue that some unionines (e.g., *Elliptio*, *Lexingtonia*, *Pleurobema*) that use only the outer gills as marsupia may warrant a fourth subfamily--the Pleurobeminae. Spawning appears to be dependent on the temperature (Zale and Neves 1982, Bruenderman and Neves 1993) but may also be influenced by stream discharge (Hove and Neves 1994). Fertilization rates are dependent on the spatial aggregation of reproductive adults (Downing et al. 1993).

Mussels are generally categorized as either short-term summer brooders (tachytictic) or long-term winter brooders (bradytictic) (Neves and Widlak 1988). Tachytictic species have a spring fertilization period; the glochidia are then incubated for a few months and are expelled during the summer or early fall. Bradytictic species have a late summer or early fall fertilization period, with the glochidia incubating over winter, and are expelled the following spring or early summer.

The fact that some species have glochidia that overwinter on hosts (e.g., Watters and O'Dee 1997) indicates that they do not clearly fall into either the tachytictic or bradytictic reproductive strategy. This has led Watters and O'Dee (2001) to believe that glochidial release is more a function of water temperature. They have coined new terms to better coincide with the actual reproductive strategies of mussels. Winter releasers expel glochidia when water temperatures dip below a threshold level, while summer releasers expel glochidia when water temperatures rise above a threshold level. The reproductive strategy where glochidia have been released in the autumn or winter to parasitize hosts (winter releasers) is termed host overwintering. This is in contrast with the strategy of parent overwintering, whose species are summer releasers. Although parent overwintering is typically associated with bradyticty, species that are strictly tachytictic may also be summer releasers (Watters and O'Dee 2001).

After a variable incubation period, mature glochidia, which may number in the tens of thousands to several million (Surber 1912, Coker et al. 1921, Yeager and Neves 1986), are expelled into the water column. The temporal release of glochidia is thought to be behavioral rather than developmental (Gordon and Layzer 1993). Glochidia must come into contact with specific species of fish whose gills and fins they temporarily parasitize, although two species have been shown to possibly utilize amphibian hosts (Howard 1915, 1951; Watters 1997). Some mussel species, such as *Lasmigona subviridis* (Conrad, 1835), *Strophitus undulatus* (Say 1817), and *Utterbackia imbecillis* (Say 1829), may not require a host fish to complete their life cycle (Lefevre and Curtis 1912, Howard 1914; G. T. Watters, Ohio Biological Survey, pers. comm., 1998). Glochidia failing to come into contact with a suitable host will drift through the water column, surviving for only a few days at most (Sylvester et al. 1984; Neves and Widlak 1988; Jansen 1990; O'Brien, in press).

Glochidia are generally released individually in netlike mucoid strands that entangles fishes (Haag and Warren 1997) or as discreet packets, termed "conglutinates," which represent all the glochidial contents (and sometimes eggs) of a single water tube packaged in a mucilaginous capsule (Ortmann 1910, 1911). A newly described method, termed a "superconglutinate" by Williams and Butler (1994), involves the expulsion of the sum of the conglutinates from discreet portions of both outer gills that are packaged in a single glochidial mass (Haag et al. 1995, Hartfield and Butler 1997, Haag et al. 1999, O'Brien and Brim Box 1999).

Each of the three basic methods of glochidial expulsion and glochidial shape facilitates attachment to specific host fish and to specific fish structures (fin versus gill), respectively (Lefevre and Curtis 1910, 1912). Although supported by field observations (Lefevre and Curtis 1912, Neves and Widlak 1988), the fish structure parasitized may in some cases be due to fish behavior rather than morphology (Gordon and Layzer 1989). Anodontines are generally bradytictic (Zale and Neves 1982), broadcasting masses of hooked glochidia in netlike mucoid strands (Haag and Warren 1997) that generally parasitize the fins of fishes (Clarke 1981, Haag and Warren 1997).

Species in the subfamily Unioninae are generally tachytictic and package their glochidia in a conglutinate, which are expelled out of the excurrent aperture (Neves and Widlak 1988). Conglutinates often resemble colorful fish prey items (e.g., worms, insect larvae, fish fry) (Chamberlain 1934, Luo 1993, Hartfield and Hartfield 1996), and researchers have demonstrated that conglutinates are actively foraged by fish (Ortmann 1911, Neves and Widlak 1988, Weiss and Layzer 1995, Haag and Warren 1997). Unionine glochidia are hookless and generally parasitize gills (Neves et al. 1985).

The Lampsilinae are generally bradytictic (Zale and Neves 1982); they utilize discreet portions of the outer pair of gills as marsupia (Ortmann 1911) and employ two methods of glochidial release. Lampsilines that have mantle modifications (e.g., *Lampsilis*, *Medionidus*) to attract fish generally do not release conglutinates; rather, they expel loose masses of glochidia out openings in the ends of the water tubes (Ortmann 1910, Neves and Widlak 1988, Richard et al. 1991). Mantle modifications include flaps, or villi (elongate papilla-like structures), exhibiting bright colors, rhythmic movements, and/or actual mimicry of fish prey items (e.g., worms, insect larvae, fish fry [complete with an eyespot]) that serve to attract host fish (Ortmann 1911, Coker et al. 1921, Chamberlain 1934, Kraemer 1970, Zale and Neves 1982, Hartfield and Hartfield 1996, Barnhart and Roberts 1997, Haag and Warren 1999, Haag et al. 1999). The mantle displays of two species of *Villosa* took place during the day for one species and at night for the other, suggesting that display times may be species specific (Haag and Warren 2000).

Mantle displays have been shown to actively elicit attacks from fish (Haag and Warren 1999), and mantle lures potentially reduce the chances that glochidia will infest an unsuitable fish host (Haag et al. 1999). Laboratory tests have demonstrated that the presence of fish, and especially direct physical contact of host fish with mantle lures, stimulated larger releases of glochidia than when fish were absent or no physical contact occurred (Haag and Warren 2000). In the presence of fish, the swollen marsupialized gills are often extruded well beyond the edge of the shell margins between the mantle “lures” (Kraemer and Swanson 1985). Light-sensitive areas on the mantle may be stimulated by the shadow of a passing fish (Kraemer 1970, Jansen 1990, Weiss and Layzer 1995). When the mantle lure is attacked by a fish, a cloud of hookless glochidia is released into the buccal cavity, thus facilitating gill infestation. Lampsilines that lack mantle modifications (e.g., *Ptychobranchus*, *Obliquaria*, *Cyprogenia*) expel their glochidia as conglutinates, as do the Unionines outlined above.

A small group of lampsilines expel superconglutinates (Haag et al. 1995, Hartfield and Butler 1997, Haag et al. 1999, O’Brien and Brim Box 1999). The superconglutinate, which is tethered by a secreted transparent mucilaginous strand that may reach 8 feet in length, resembles a fish in size, shape, and coloration, complete with stripes and an eyespot. During the production of the superconglutinate, the water currents move the fish mimic in motions that are similar to a small fish (Haag et al. 1995, Hartfield and Butler 1997). Once detached from the female, the fate of the superconglutinate depends on the chance that the current will wrap it around a rock, branch, or any structure in the stream where it will continue to mimic prey for a piscivorous host fish (Haag et al. 1995).

As few as 1 to as many as 25 fish species are known to serve as suitable hosts for particular species of mussels (Fuller 1974, Gordon and Layzer 1989). Host specificity appears to be common in mussels (Neves 1993), with most species utilizing only a few host fishes (Lefevre and Curtis 1912, Zale and Neves 1982, Yeager and Saylor 1995). Research on these five species seems to corroborate this assertion (see “Reproductive Biology of the Five Species”).

There are two types of fish immunity to glochidial infestation--natural and acquired (Watters and O’Dee 1996). Natural immunity is believed to be a tissue response (Bauer and Vogel 1987), where attempts to parasitize nonhost fish will result in rejection and glochidial death by the host’s immune system, usually within 11 days (Neves et al. 1985, Yeager and Neves 1986, Waller and Mitchell 1989). However, chemically induced metamorphosis (which may prove to be a useful artificial propagation tool in cases where the host fish is not known) has been accomplished in certain species (Kirk and Layzer 1997). In the case of acquired immunity, even a suitable host fish will display decreased transformation rates with subsequent infections (Arey 1932, Bauer and Vogel 1987, Luo 1993). The number of exposures needed to initiate glochidial sloughing is highly variable (Watters and O'Dee 1996).

The parasitic stage generally lasts a few weeks (Neves et al. 1985, O'Brien, in press), but can last much longer (Yeager and Saylor 1995, Haag and Warren 1997), and is temperature-dependent (Watters and O'Dee 2001). After dropping from fish hosts, newly metamorphosed juveniles passively drift with currents and ultimately settle in depositional areas with other suspended solids (Neves and Widlak 1987, Yeager et al. 1994). Juveniles must, however, come into contact with suitable habitat to begin their free-living existence (Howard 1922). Survival rates for a glochidium to metamorphosis ranges from 0.000001 to 0.0001 percent, not factoring in predation after metamorphosis (Watters and Dunn 1993-94).

Glochidial parasitism serves as a means of dispersal for this relatively sedentary group (Neves 1993). The intimate relationship between mussels and their host fish has therefore played a major role in mussel distributions on both a geographic (Watters 1992) and community (Haag and Warren 1998) scale. Haag and Warren (1998) determined that mussel community composition was more a function of fish community pattern variability than of microhabitat variability and that the type of strategy used by mussels for infecting host fishes was the determining factor. Host-generalist mussels without elaborate host-attracting mechanisms (e.g., anodontines) and host-specialized mussels with elaborate host-attracting mechanisms (e.g., lampsilines) were independent of host-fish densities. Conversely, host-specialist mussels without elaborate host-attractant mechanisms (e.g., unionines) were dependent on densities of host fishes. Stable numbers of hosts therefore appear to be critical for determining where unionines (e.g., rough rabbitsfoot) are able to persist (Haag and Warren 1998).

Knowledge about the reproductive biology of many freshwater mussels remains incomplete (Jansen 1990). For example, according to Watters (1994), host fish for only 25 percent of the 300 mussel species in North America have been identified, although subsequent studies are gradually expanding that number (e.g., Luo 1993, Weiss and Layzer 1995, Yeager and Saylor 1995, Watson and Neves 1996, Haag and Warren 1997, Howells 1997, Keller and Ruessler 1997, Roe and Hartfield 1997, Haag et al. 1999, O'Dee and Watters 2001, various unpublished reports in the Triannual Unionid Report). Host fish information is lacking most in the Southeast, where more than 90 percent of the freshwater mussel species occur (Neves et al. 1997).

Reproductive Biology of the Five Species

Cumberland elktoe

Gordon and Layzer (1993) summarized the reproductive biology and identified fish hosts of the Cumberland elktoe. This anodontine species was found gravid from October through May, but they observed no fish infested with its glochidia until March. They found Cumberland elktoe glochidia to develop equally well on both fin and gill surfaces. Five native fish species were parasitized by Cumberland elktoe glochidia--whitetail shiner (*Cyprinella galactura*), northern hogsucker (*Hypentelium nigricans*), rock bass (*Ambloplites rupestris*), longear sunfish (*Lepomis megalotis*), and rainbow darter (*Etheostoma caeruleum*). However, under laboratory conditions, juvenile specimens transformed only on the northern hogsucker (Gordon and Layzer 1993). The period of glochidial encystment (i.e., until transformation into free-living juveniles) took 24 days, at 66.2° ± 5.4°F.

Oyster mussel

Spawning probably occurs in the lampsiline oyster mussel in late spring or early summer, as glochidia have been observed in the marsupia during May, June, and July (Gordon and Layzer 1989). In the Powell River, Yeager and Saylor (1995) found 58 percent of the females gravid in May (water temperature from 59.0° to 64.0°F). The age of gravid females, using the external growth ring method (Chamberlain 1931, Crowley 1957), was estimated at 7 to 10 years. The glochidia are likely released in early summer (Gordon and Layzer 1989). Approximately 12,000 to 16,000 glochidia per female have been observed (Neves, pers. comm., 2000). Seven native fish species have been identified as hosts--the wounded darter (*Etheostoma vulneratum*), redline darter (*E. rufilineatum*), bluebreast darter (*E. camarum*), dusky darter (*Percina sciera*), banded sculpin (*Cottus carolinae*), black sculpin (*C. baileyi*), and mottled sculpin (*C. bairdi*) (Yeager and Saylor 1995; J. Jones and Neves, USGS, unpublished data, 1998). Transformation took from 19 to 34 days, at 60.4° to 62.4°F (Yeager and Saylor 1995).

Cumberlandian combshell

Spawning in the lampsiline Cumberlandian combshell probably occurs in late summer with the glochidia being held over winter and released in late spring (Gordon 1991). Gravid females have been reported from early May to June at water temperatures of 59.0° to 64.0°F) (Ahlstedt 1991a, Yeager and Saylor 1995). Estimated age (see Chamberlain 1931, Crowley 1957) of gravid females was 8 to 13 years. Several native host fish species have been identified, including the wounded darter, redline darter, bluebreast darter, snubnose darter (*E. simoterum*), greenside darter (*E. blennioides*), logperch (*Percina caprodes*), banded sculpin, black sculpin, and mottled sculpin (Yeager and Saylor 1995; Jones and Neves, USGS, unpublished data, 1998). Transformation took from 16 to 48 days, at 60.4° to 62.4°F (Yeager and Saylor 1995).

Purple bean

Gravid females of the purple bean, another lampsiline, have been observed in January and February (Ahlstedt 1991a; Butler, pers. obs., 2001). At least three host fish species have been identified--the fantail darter (*Etheostoma flabellare*), greenside darter, and mottled sculpin and/or banded sculpin (Watson and Neves 1996). Transformation took from 11 to 25 days, at 70.7° to 76.1°F.

Rough rabbitsfoot

Yeager and Neves (1986) summarized the reproductive biology and identified fish hosts of the unionine rough rabbitsfoot. Spawning occurred from May through June (water temperature 68.0° to 71.6°F). Fertilization success was high (>95 percent) through late June, but by July only unfertilized ova were found. Unlike most unionines, 65 percent of 82 gravid females examined utilized only the outer demibranchs as marsupia. They estimated gravidity rates (30 to 60 percent) peaked in late May then gradually declined. Females release lanceolate-shaped whitish to reddish brown conglutinates (0.4 inch long) that contain 375 to 505 semicircular-shaped glochidia. Fecundity was estimated at 115,000 embryos per female. The estimated age (see Chamberlain 1931, Crowley 1957) of gravid females was 10 to 22 years. Three cyprinid host fish species have been identified--the whitetail shiner, spotfin shiner (*C. spiloptera*), and bigeye chub (*Hybopsis amblops*). Infestation rates ranged from as few as five to ten glochidia on individual fishes. Transformation took from 13 to 23 days, at 68.9° to 71.4°F.

REASONS FOR DECLINE

Past and Present Threats

Two general categories of factors have impacted freshwater mussel resources for the past 500 years in Eastern North America--exploitation and habitat alteration. The former category primarily includes activities associated with the post-Mississippian Culture; pearling; the pearl button industry; and, more recently, the cultured pearl industry. Anthony and Downing (2001) provide a detailed summary of these three endeavors. The latter category includes a variety of anthropogenic activities prevalent during the past two centuries.

EXPLOITATION

Native Americans

The Mississippian Culture and Native Americans that followed in the Southeast used mussels in a variety of ways (Parmalee and Bogan 1998, Davis 2000). They made decorative shell jewelry such as gorgets (worn by chieftains) and drilled pearl necklaces; fashioned scrapers, hoes, utensils, and other tools from shells, and incorporated crushed shells as a way of strengthening their pottery.

But the foremost use of mussels by Native Americans was as food (Parmalee and Klippel 1974). Shell or kitchen middens of discarded mussels along large preimpounded rivers in the region stand as evidence for the prevalence of this activity and the abundance of the resource. Davis (2000) stated that "[t]he survival of [post-]Mississippian material culture--at least as practiced during the sixteenth century--was therefore closely linked to the mussels' presence and availability." Archaeological evidence suggests that mussels were commonly steamed open for consumption (Morrison 1942).

Middens excavated from the Tennessee River have contained tremendous numbers of mussels and covered areas up to 3 to 4 acres in size in deposits 3 to 15 feet in depth (Cahn 1936a). Their size indicates that some middens may have been created over several decades or possibly centuries. One large Tennessee River midden near the mouth of the Flint River in Alabama was estimated to contain 9.9 million mussels (Cahn 1936a). Despite the fact that hundreds of millions of mussels must have been harvested for food from the Tennessee River alone, the mussel resource was not destroyed nor a single species lost (Cahn 1936a). However, the low nutritional value of mussels indicates that they were important only as a seasonal food supplement (Parmalee and Klippel 1974).

Pearling

Pearling has its roots hundreds, if not thousands, of years ago (Anthony and Downing 2001). The post-Mississippian Cultures of the Southern Appalachian region traded pearls with the Spanish in the early 1500s (Davis 2000). Caches of pearls weighing more than a hundred pounds have been documented in Native American villages in the Southeast. In the latter half of the eighteenth century, pearling made a resurgence in various areas, usually being sparked by the fortuitous discovery of a large, valuable specimen (Parmalee and Bogan 1998). According to Anthony and Downing (2001), virtually all mussel species were exploited for their pearls, although some species were more actively sought than others. Profits from late nineteenth century "pearl rushes" were relatively substantial, surpassing profits derived from mining and petroleum production (Claassen 1994).

By 1860, pearlers were extensively harvesting mussels for pearls in Kentucky, Tennessee, and several other states (Anthony and Downing 2001). The Caney Fork was considered by Myer (1914) to be the birthplace of the Cumberlandian Region's pearling industry. Wilson and Clark (1914) reported numerous sites along the Cumberland River where pearling was active. The Muscle Shoals area of northern Alabama was also an important center of pearling.

Although pearls were collected from nearly all the major Southern Appalachian streams, the lower Clinch and Emory Rivers became the "economic heart" of the pearl industry (Davis 2000). According to Davis (2000), place names along the Clinch River were sometimes based on the names of commonly found mussels. These included Blue-Point (for *Amblema plicata*, the threeridge), Buckhorn (for *Tritogonia verrucosa*, the pistolgrip), Butterfly (for *Ellipsaria lineolata*), and Pancake (for *Potamilus alatus*, the pink heelsplitter). Hundreds of residents would camp along the river during low water periods or gather for special events to search for mussels yielding pearls, with exceptional specimens bringing a thousand dollars or more (Kunz and Stevenson 1908). Boepple and Coker (1912) reported a particularly habitat disruptive method of harvest where "a plow drawn by a strong team" was sometimes used in shallow Clinch River shoals enabling harvesters to pick up mussels that had been buried in the substrate.

Considering that perhaps only 1 in 10,000 (McGregor and Gordon 1992) to 1 in 15,000 (Anthony and Downing 2001) mussels may produce a commercially valuable pearl, it may be safe to assume that hundreds of thousands, if not millions, of mussels were sacrificed in regional streams by individuals hoping to "get rich quick." Some rivers were reported to have "practically been depleted" of mussels by pearlers (Hickman 1937). Although not included in a list of the most actively sought species for pearls (Anthony and Downing 2001), large specimens of both the thick-shelled Cumberlandian combshell and rough rabbitsfoot may have been among the species exploited for pearls. Major impoundments in the Cumberlandian Region effectively sealed the fate of the pearling industry in the early part of the twentieth century (Neves 1999b, Davis 2000).

Pearl Buttons

The making of pearl buttons, which utilized the shells of specific mussel species as a raw material, began commercially in the late 1880s (Anthony and Downing 2001). Production rates and the extent to which the industry exploited mussel beds has been well documented (Claassen 1994, Anthony and Downing 2001). At least one button factory was located in the region, in Clinton, Tennessee, on the lower Clinch River (S. A. Ahlstedt, USGS, pers. comm., 2002). Annual button production topped out at over 5.75 billion during 1916 (Classen 1994) worth more than $175 million in 1998 dollars (Anthony and Downing 2001). Pearls represented a valuable fringe resource from mussels harvested for buttons, and composed up to one-third of the average commercial musseler's annual income until about 1921 (Anthony and Downing 2001).

Although none of the five species addressed in this recovery plan were included in a list of 50 mussel species "heavily exploited during the first half of the [twentieth] century" for buttons, many other species of mussels were likely killed as by-catch (Anthony and Downing 2001). The pearl button industry flourished for about 35 years and died out over the next two decades due to overexploitation of large, high-quality shells; foreign competition (mostly from Japan); and the advent of plastic buttons (Anthony and Downing 2001).

Cultured Pearls

The slow demise of the pearl button industry provided the blossoming cultured pearl industry with an opportunity for the alternate use of large numbers of freshwater mussel shells (Anthony and Downing 2001). Spherical beads fashioned from mussel shells have served as nuclei for pearls cultured from Pacific basin oysters since the 1920s. Globally, cultured pearls represent a three billion dollar industry employing hundreds of thousands of workers (Hubbs and Jones 1996). Although the overall value of the global cultured pearl industry is huge, the shell export portion of this venture centered in the lower Tennessee River is a much smaller industry, even when compared to the peak of the pearl button industry (Anthony and Downing 2001)." Although larger specimens of the Cumberlandian combshell may have been harvested occasionally for buttons, it is doubtful that any of the five species addressed in this recovery plan have been overly exploited for these endeavors.

Summary

Despite the compelling mussel exploitation argument outlined by Anthony and Downing (2001) and the hundreds of millions of mussels harvested for food by Native Americans in the Tennessee River alone, overharvesting has not been implicated in the extinction of any freshwater mussel, nor any other Temperate Zone stream organism (Allan and Flecker 1993). The three dozen freshwater mussels thought to be extinct (see "Background") have all been driven out of existence by forces featured in the following section on "Habitat Alteration." The harvest of Cumberlandian Region mussel species for commercial purposes is well documented. It is doubtful, however, that the five species addressed in this recovery plan have ever been overly exploited for pearling, pearl buttons, cultured pearls, or any other exploitative activity.

HABITAT ALTERATION

Resource managers should realize that, in the majority of cases, mussel resources were widely sustained during human interactions throughout history despite the widespread, prolonged, and sometimes dramatic exploitation events outlined in the previous section. Rather, the collapse of the mussel fauna outlined in the "Background" section of this plan is by and large the result of the second broad category of impacts--habitat loss from human-induced degradation (Williams et al. 1993, Neves 1993). Principal causes include impoundments, channelization, pollution, and sedimentation that have altered or eliminated those habitats that are essential to the long-term viability of many riverine mussel populations. Neves et al. (1997) and Watters (2000) summarized many of these major categories of impacts, while Richter et al. (1997) identified specific stressors that threatened imperiled mussels and other aquatic species.

The mussel fauna of the Cumberlandian Region is no exception to this long-standing and general status trend (Neves 1991). From observations made at the turn of the century, Adams (1915) commented on mine waste, industrial contamination, deforestation, and resulting sedimentation in the upper Tennessee River system. Coupled with the increased susceptibility that certain species have to environmental perturbations, particularly members of the genus *Epioblasma* (Dennis 1987, Neves et al. 1997), it is not difficult to realize the plight of mussels stemming from major habitat alterations.

Impoundments

The effects of dams, hydrological disturbances, and other in-stream alterations of riverine habitat have been reviewed by numerous authors, including Ellis (1942), Baxter (1977), and Yeager (1993, 1994). Neves et al. (1997) and Watters (2000) reviewed the specific effects of impoundments on freshwater mollusks. Ortmann (1909) may have been the first biologist to correctly assess, but significantly underestimate, the impact of dams on the aquatic biota (Stansbery 1970). Impoundments, especially large main-stem reservoirs, have significantly altered riverine ecosystems (Baxter and Glaude 1980, Williams et al. 1992, Allan and Flecker 1993, Ligon et al. 1995, Sparks 1995) and have been a major factor in the high extinction rate of freshwater mollusks (Johnson 1978, Lydeard and Mayden 1995, Neves et al. 1997).

Impoundments result in the elimination of riffle and shoal habitats and the subsequent loss of mussel resources (Ortmann 1925; van der Schalie 1938; Scruggs 1960; Bates 1962; Neel 1963; Isom 1969, 1971; Stansbery 1970, 1973b; Fuller 1974; Schmidt et al.

1989; Williams et al. 1992; Layzer et al. 1993; Parmalee and Hughes 1993; Lydeard and Mayden 1995; Sickel and Chandler 1996; Watters 1996). Most of a river's ecological processes are also disrupted, for example, by modifying flood pulses; controlling impounded water elevations; increasing depth; decreasing habitat heterogeneity; altering water flow, sediment, nutrients, energy input and output, and the riverine biota; and causing the loss of bottom stability due to subsequent sedimentation (Williams et al. 1992, Ligon et al. 1995, Sparks 1995). Most riverine species are unable to successfully reproduce and recruit under reservoir conditions (Fuller 1974, Neves et al. 1997, Hughes and Parmalee 1999), including these five species.

In addition, dams can seriously alter downstream water quality and riverine habitat (Allan and Flecker 1993, Ligon et al. 1995, Collier et al. 1996) and negatively impact mussel populations in tailwaters (Cahn 1936b, Hickman 1937, Ahlstedt 1983, Miller et al. 1984, Layzer et al. 1993, Heinricher and Layzer 1999, McMurray et al. 1999b, Vaughn and Taylor 1999). These changes include thermal alterations (Neves 1993), channel characteristics, habitat availability, and flow regimes that have drastic effects on the stream biota (Krenkel et al. 1979, Allan and Flecker 1993). Altered effects also include fish community shifts (Brim 1991) and the resultant colonization by fewer native species and more nonindigenous species (Williams and Neves 1992). Daily discharge fluctuations, bank sloughing, seasonal oxygen deficiencies, cold-water releases, turbulence, high silt loads, and altered host fish distribution have contributed to limited mussel recruitment and skewed demographics (Sickel 1982, Ahlstedt 1983, Miller et al. 1984, Layzer et al. 1993, McMurray et al. 1999b).

Cold-water releases from large nonnavigational dams are the result of placing water intake structures low on the dam to increase hydropower efficiency (Krenkel et al. 1979). The release of cold water and scouring of the riverbed from highly fluctuating, turbulent flows in tailwaters have also been implicated in the demise of Cumberlandian Region mussel faunas (Miller et al. 1984, Layzer et al. 1993, Heinricher and Layzer 1999).

Specifically, tachytictic species, which depend on warm summer temperatures to initiate gametogenesis, spawning, glochidia release, and the proper host fish being present, experience reproductive failure below dams (Heinricher and Layzer 1999). Bradytictic species are also negatively affected, and the decline of mussel populations has been manifested over a period of several decades (Neves 1999a). The mussel faunas of the middle Cumberland, lower Obey, lower Caney Fork, and Elk Rivers have been profoundly impacted by cold-water releases, including populations of the Cumberlandian combshell and oyster mussel.

The entire length of the main stems of the Tennessee and Cumberland Rivers and many of their largest tributaries are now impounded or greatly modified by the discharge of tailwaters. More than 2,300 river miles (about 20 percent) of the Tennessee River and its tributaries with drainage areas of 25 square miles or greater were impounded by the TVA by 1971 (TVA 1971). The subsequent completion of additional major impoundments on tributary streams (e.g., Duck River in 1976 and Little Tennessee River in 1979) significantly increased the total miles impounded behind the 36 major dams in the Tennessee River system (Neves et al. 1997). Approximately 90 percent of the 562-mile length of the Cumberland River downstream of Cumberland Falls is either impounded (three locks and dams and Wolf Creek Dam) or otherwise adversely impacted by cold-water discharges from Wolf Creek Dam. Miller et al. (1984) located only two mussel specimens in a survey below Wolf Creek Dam covering 68 miles of river that formerly harbored 39 species (Neel and Allen 1964). Other major U.S. Army Corps of Engineers (Corps) impoundments on Cumberland River tributaries (e.g., Laurel River, Obey River, Caney Fork, Stones River) have inundated more than 125 miles of potential riverine habitat for the Cumberland elktoe, oyster mussel, and Cumberlandian combshell.

Impoundments, as barriers to dispersal, contribute to the loss of local populations by blocking postextirpation recolonization (Luttrell et al. 1999). Population losses due to impoundments have probably contributed more to the decline of the Cumberlandian combshell, oyster mussel, and rough rabbitsfoot and most other Cumberlandian Region mussels than any other single factor (as the Cumberland elktoe and purple bean generally inhabit smaller rivers, impoundments have had less of an impact on them). Many populations of these species have been isolated due to impoundments (see "Patterns of Imperilment," "Narrative Outline," and Recovery Task 1.3.6 for a discussion of the consequences of population fragmentation).

Channelization

Dredging and channelization activities have profoundly altered riverine habitats nationwide, with effects on streams summarized by Simons (1981), Bhowmik (1989), and Hubbard et al. (1993). DeHaan (1998) provided an annotated bibliography of sediment transport and deposition in large rivers. Hartfield (1993) and Neves et al. (1997) reviewed the specific effects of channelization on freshwater mollusks. Channelization impacts a stream's physical (e.g., accelerated erosion, reduced depth, decreased habitat diversity, geomorphic instability, riparian canopy loss) and biological (e.g., decreased fish and mussel diversity, changed species composition and abundance, decreased biomass and growth rates) characteristics (Stansbery and Stein 1971, Hartfield 1993, Hubbard et al. 1993). Channel construction for navigation has been shown to increase flood heights (Belt 1975), thus exacerbating flood events that convey to streams large quantities of sediment with adsorbed contaminants. Channel maintenance may also result in downstream impacts (Stansbery 1970), such as increases in turbidity and sedimentation, which may smother benthic organisms. Although the volume of literature demonstrating the on-site and off-site environmental and economic consequences of dredging for navigation and flood control is substantial (Smith and Patrick 1991), these activities continue in the Southeast.

Mineral Extraction

Heavy metal-rich drainage from coal mining and associated sedimentation have adversely impacted many stream reaches (Barnhisel and Massey 1969, Ahmad 1973, Curry and Fowler 1978), destroying mussel beds and preventing natural recolonization (Simmons and Reed 1973, McCann and Neves 1992). Neves et al. (1997) reviewed the effects of various mining activities on freshwater mollusks. The low pH commonly associated with mine run-off can lead to an inability of glochidia to clamp their valves on host tissues thus preventing proper encystment (Huebner and Pynnönen 1992). Acid mine run-off may thus be having local impacts on recruitment of, particularly, the Cumberland elktoe, since most of its range is within watersheds where coal mining is still occurring.

Impacts associated with coal mining activities have particularly altered upper Cumberland River system streams with diverse historical mussel faunas (Stansbery 1969, Blankenship 1971, Blankenship and Crockett 1972, Starnes and Starnes 1980, Schuster et al. 1989, Anderson et al. 1991) and have been implicated in the decline of *Epioblasma* species, especially in the Big South Fork (Neel and Allen 1964). Strip mining continues to threaten mussels in coal field drainages of the Cumberland Plateau (Anderson 1989, Warren et al. 1999), including Cumberland elktoe, oyster mussel, and Cumberlandian combshell populations. The Marsh Creek population of the Cumberland elktoe has also been adversely affected and is still threatened by potential spills from oil exploration activities. Circumstantial evidence indicates that salinity, a by-product of oil exploration activities, is lethal to some glochidia (Liquori and Insler 1985).

The role that coal mining has played in the decline of mussel fauna in the Powell River in Virginia was prophesied by Ortmann (1918) and has been briefly summarized by Wolcott and Neves (1991, 1994). Five mine tailings pond spills were reported from 1995 to 1999 in the upper Clinch and Powell River systems (Hampson et al. 2000), at least one of which resulted in a major fish kill (Koch, pers. comm., 1996). Research by Kitchel et al.

(1981) indicates that Powell River mussel populations were inversely correlated with coal fines in the substrate. When coal fines were present, decreased filtration times and increased movements were noted in laboratory-held mussels (Kitchel et al. 1981). Polycyclic aromatic compounds (PAHs) are indicative of coal fines in the bottom sediments of streams. Known to be toxic to mussels and fishes, PAHs have been found at relatively high levels in the upper portions of the Clinch and Powell Rivers in Virginia (Hampson et al. 2000). In a quantitative study in the Powell River, Ahlstedt and Tuberville (1997) attributed a 15-year decline of the oyster mussel, Cumberlandian combshell, and rough rabbitsfoot and the long-term decrease in species diversity (from 30 in 1979 to 21 in 1994) to general stream degradation due primarily to coal mining activities in the headwaters. Mining activities also likely contributed to the extirpation of the purple bean from the Powell River several decades ago. Iron and phosphate mining in the Duck River watershed was thought to have caused mussel declines in the early 1900s (Ortmann 1924).

Gravel Mining

In-stream gravel mining has been implicated in the destruction of mussel populations (Stansbery 1970, Yokley and Gooch 1976, Grace and Buchanan 1981, Hartfield and Ebert 1986, Schuster et al. 1989, Hartfield 1993, Howard 1997). Lagasse et al. (1980), Kanehl and Lyons (1992), and Roell (1999) reviewed the physical and biological effects of mining sediment from streams. Negative impacts include riparian forest clearing (e.g., mine site establishment, access roads, lowered floodplain water table); stream channel modifications (e.g., geomorphic instability, altered habitat, disrupted flow patterns [including lowered elevation of stream flow], sediment transport); water quality modifications (e.g., increased turbidity, reduced light penetration, increased temperature); macroinvertebrate population changes (e.g., elimination, habitat disruption, increased sedimentation); and changes in fish populations (e.g., impacts to spawning and nursery habitat, food web disruptions) (see discussion in "Sedimentation"). Once mussels have been eliminated, a decade or more may pass before recolonization occurs (Stansbery 1970, Grace and Buchanan 1981). Substrate disturbance and sedimentation impacts can also be realized for considerable distances downstream (Stansbery 1970), and possibly upstream (Hartfield 1993).

Gravel mining activities threaten the Cumberlandian combshell populations in the Powell River and in Buck Creek, the latter stream representing one of only two remaining populations of this species in the entire Cumberland River system. Mining activities on the Elk River (Ahlstedt 1991b) may have played a role in the extirpation of the oyster mussel and Cumberlandian combshell from that river. Gravel removal was apparent at 12 sites along a 40-mile stretch of the lower Elk River during 1999 mussel sampling (Anonymous 1999). Activities that occur without a permit, unless controlled, may prevent the long-term reintroduction of many federally listed mussels (13 species are known) into that stream.

Contaminants

Contaminants contained in point and nonpoint discharges can degrade water and substrate quality and adversely impact, if not destroy, mussel populations (Horne and McIntosh 1979, Neves and Zale 1982, McCann and Neves 1992, Havlik and Marking 1987). Although chemical spills and other point sources of contaminants may directly result in mussel mortality, widespread decreases in density and diversity may result in part from the subtle, pervasive effects of chronic, low-level contamination (Naimo 1995). The effects of heavy metals and other contaminants on freshwater mussels were studied by Mellinger (1972), Fuller (1974), Havlik and Marking (1987), Naimo (1995), Keller and Lydy (1997), and Neves et al. (1997).

Mussels appear to be among the most intolerant organisms to heavy metals (Keller and Zam 1991), several of which are lethal, even at relatively low levels (Havlik and Marking

1987). Cadmium appears to be the heavy metal most toxic to mussels (Havlik and Marking 1987), although chromium, copper, mercury, and zinc also negatively affect biological processes (Jacobson et al. 1993, Naimo 1995, Keller and Zam 1991, Keller and Lydy 1997). In laboratory experiments, mussels suffered mortality when exposed to 2.0 parts per million (ppm) cadmium, 12.4 ppm chromium, 19.0 ppm copper, and 66.0 ppm zinc (Mellinger 1972, Havlik and Marking 1987). Most metals are persistent in the environment (Miettinen 1977), remaining available for uptake, transportation, and transformation by organisms for long periods (Hoover 1978). Metals stored in mussel tissues indicate recent or current exposure (Havlik and Marking 1987), while concentrations in shell material indicate past exposure (Imlay 1982, Mutvei et al. 1994). Highly acidic pollutants such as metals are capable of contributing to mortality by dissolving mussel shells (Stansbery 1995).

Among other pollutants, arsenic trioxide has been shown to be lethal to mussels at concentrations of 16.0 ppm and ammonia at concentrations of 5.0 ppm (Havlik and Marking 1987). Arsenic is commonly used in the poultry industry as a food additive for enhancing growth, while ammonia is oftentimes associated with animal feedlots, nitrogenous fertilizers, and the effluents of older municipal wastewater treatment plants. In stream systems, ammonia is most prevalent at the substrate/water interface (Frazier et al. 1996). Due to its high level of toxicity and the fact that the highest concentrations occur in the microhabitat where mussels live, ammonia should be considered among the factors potentially limiting survival and recovery of mussels at some locations (Augspurger et al., in prep.).

Certain adult species may tolerate short-term exposure (Keller 1993). However, the effects of heavy metals and other toxicants are especially profound on juvenile mussels (Robison et al. 1996) and on the glochidia, which appear to be very sensitive to toxicants such as ammonia (Goudreau et al. 1993). Low levels of some metals may inhibit glochidial attachment (Huebner and Pynnönen 1992). Juvenile mussels may inadvertently ingest contaminated silt particles while feeding (see “Food Habits”). Mussel recruitment may therefore be reduced in habitats with low but chronic heavy metal and other toxicant inputs (Yeager et al. 1994, Naimo 1995, Ahlstedt and Tuberville 1997), which may have contributed to the demise of these five species.

Contaminants associated with households and urban areas, particularly those from industrial and municipal effluents, may include heavy metals, ammonia, chlorine, phosphorus, and numerous organic compounds. Run-off from urban areas tends to have the highest levels of many pollutants, such as phosphorus and ammonia, when compared to other catchments (Mueller et al. 1995). Collectively, these pollutants may cause decreased dissolved oxygen levels, increased acidity, and other water chemistry changes that may be lethal to mussels (Horne and McIntosh 1979, Rand and Petrocelli 1985, Sheehan et al. 1989, Keller and Zam 1991, Dimock and Wright 1993, Goudreau et al. 1993, Jacobson et al. 1993, Keller 1993).

Sediment from the upper Clinch River, where several of these species occur, was found to be toxic to juvenile mussels (Robison et al. 1996). Ahlstedt and Tuberville (1997) speculated that the presence of toxins in the Clinch River may explain the decline and lack of mussel recruitment at some sites in the Virginia portion of that stream. Wilcove and Bean (1994) reported that tests with the effects of copper on Clinch River mussels proved toxic at levels below U.S. Environmental Protection Agency (EPA) established criteria.

Although the Clean Water Act (CWA) has helped eliminate many point-source effluents, “straight pipes” (pipelines conveying untreated household effluents from rural homes directly into streams) continue to discharge wastes. Fraley and Ahlstedt (2001) thought that straight pipes were partially to blame for the documented decline of the native mussel fauna in Copper Creek from 19 species in 1980 to 11 species in 1998. Included in the historical Copper Creek fauna were the oyster mussel, rough rabbitsfoot, and purple bean, although only the latter species was found live in 1998. Numerous other streams in the Cumberlandian Region doubtless also have straight pipes discharging pollutants into mussel habitat.

Agricultural sources of chemical contaminants are considerable, and include two broad categories: nutrient enrichment and pesticides (Frick et al. 1998). Nutrients originate primarily from poultry farms, livestock feedlots, and fertilizers from row crop agriculture. Nitrate concentrations are particularly high in surface waters downstream of agricultural areas (Mueller et al. 1995). Stream ecosystems are impacted when nutrients are added at concentrations that cannot be assimilated (Stansbery 1995). Hoos et al. (2000) summarized data on nutrient loading in the lower Tennessee River system, where overenrichment was the cause of impairment in 37 stream segments. Nonpoint sources, primarily agricultural inputs, accounted for the largest percentage of total nitrogen and total phosphorus in all streams tested in the study area. Relatively high levels of nutrients were prevalent in the Duck River, where a large population of oystermussel occurs. Nutrient levels were also analyzed in the upper Tennessee River system by Hampson et al. (2000). Overall, nutrient concentrations were generally lower than national concentrations, and relatively high only on a localized scale.

Pesticides, primarily from row crop agriculture and secondarily from suburban areas, commonly end up in streams. Their occurrence in stream sediments and the aquatic biota was reviewed by Nowell et al. (1999). The effects of pesticides on laboratory-tested mussels may be particularly profound (Fuller 1974, Havlik and Marking 1987, Moulton et al. 1996), and commonly used pesticides have been directly implicated in a North Carolina mussel die-off (Fleming et al. 1995). Organochlorine pesticides are still detected in streams and aquatic organisms decades after their use has been banned, and may still be found at levels in streams that often exceed chronic exposure criteria for the protection of aquatic life (Buell and Couch 1995, Frick et al. 1998). Once widely used in parts of the Southeast (Buell and Couch 1995), these highly toxic compounds are persistent in the environment and partitioned into both the sediment and the lipid reservoir of organisms (Day 1990, Burton 1992). Erosion from areas of past use is a continuing source of organochlorine pesticides in some streams. Cotton is raised extensively in parts of the middle and lower Tennessee River system. One of the most important pesticides used in cotton farming, malathion, is known to inhibit physiological activities of mussels (Kabeer et al. 1979), and may decrease the ability of a mussel to respire and obtain food. This particular chemical may pose a continuing threat to the very localized population of Cumberlandian combshell in the Bear Creek system.

Toxic Spills

Numerous Cumberlandian Region streams have experienced mussel kills from toxic chemical spills and other causes (Cairns et al. 1971, Crossman et al. 1973, Neves 1986, Wolcott and Neves 1994). The high number of jeopardized species in the upper Tennessee River system make accidental spills a particular concern to conservationists and resource managers (Hampson et al. 2000). The dramatic impact the chlor-alkali chemical plant in Saltville, Virginia, has had on the aquatic fauna in the North Fork Holston River is well documented (Adams 1915; Cairns et al. 1971; Stansbery and Clench 1974; Hill et al. 1975; Ahlstedt 1980, 1991c; Neves and Zale 1982; Sheehan et al. 1989; Hampson et al. 2000). Although it is considered a chronic episode, and not an "event" like most other toxic spills, it is discussed in this section simply because of the tremendous impact it has had on the river.

Since the plant's opening in 1893, mercury and various salts (e.g., calcium chloride, sodium chloride) from this site have polluted the North Fork Holston River and decimated the entire molluscan fauna all the way to the mouth of the river, a distance of 80 miles (Ahlstedt 1991c). Occurring in this river reach were populations of the oyster mussel, Cumberlandian combshell, purple bean, rough rabbitsfoot, and 34 other mussel species (Neves and Zale 1982). From 1950 to 1971, an estimated 75 pounds of mercury per day were discharged from this facility directly into the North Fork or into unlined floodplain holding ponds (Hampson et al. 2000). The long-term kill was so thorough that only one mussel species was reported by Hill et al. (1975).

The closing of the plant in 1972 brought about the possible opportunity for natural mussel recolonization in the North Fork Holston River (Stansbery and Clench 1974). Efforts were soon made to help speed up the recovery of mussels in the North Fork. Between 1975 and 1995, three separate attempts were made transplanting thousands of specimens of 19 species of mussels (including 18 specimens of the oyster mussel; Table 2), into eight sites on the North Fork (Ahlstedt 1980, Sheehan et al. 1989, Neves 1995). Early monitoring surveys indicated that natural recolonization had not occurred by 1990 (Ahlstedt 1991c) and that transplantation success was generally very low (Sheehan et al. 1989). Surveys in the North Fork between 1991 and 1995 indicated the presence of mussels at 19 sites in Virginia below Saltville (Henley and Neves 1999). Recent recruitment, probably attributable to transplanted adults, was evident with the discovery of juveniles of four of the nine species sampled. However, the lingering effects of mercury, extremely low numbers of mussels, and possibly low numbers of fish hosts may be responsible for the general lack of mussels observed at sites within 20 miles downstream of Saltville (Henley and Neves 1995).

An alkaline fly ash pond spill in 1967 and a sulfuric acid spill in 1970 on the Clinch River at Carbo, Virginia, caused a massive mussel kill for up to 12 miles downstream from a power plant site (Cairns et al. 1971, Crossman et al. 1973, Stansbery 1986, Sheehan et al. 1989, Wilcove and Bean 1994). Populations of the oyster mussel, Cumberlandian combshell, rough rabbitsfoot, and purple bean that may have resided in the affected river reach were undoubtably impacted by these spill events. Natural recolonization has not occurred in the impacted river reach (Stansbery 1986, Ahlstedt 1991a, Hampson et al. 2000), possibly due to copper contamination from the power plant at Carbo (Wilcove and Bean 1994). An experimental reintroduction of nonlisted mussels in 1981 and 1984 has largely failed (Sheehan et al. 1989).

An overturned tanker truck resulted in a chemical spill in the upper Clinch River on August 27, 1998, killing more than 7,000 mussel specimens of 16 species. Approximately 250 specimens of three federally listed species were found dead over a 5.5-mile reach, including at least 52 purple bean specimens and 20 rough rabbitsfoot specimens (Jones et al. 2001). According to Ahlstedt (1983), "hundreds of dead shells were observed buried in the substratum" during a 1980 Elk River survey; this kill was attributed to an unknown chemical spill.

Sedimentation

Sedimentation, including siltation run-off, has been implicated as the number one factor in water quality impairment in the United States (EPA 1990). Although the specific associations that mussels have with stream substrates are poorly understood (Brim Box and Mossa 1999), sedimentation is widely thought to have contributed to the decline of mussel populations (Kunz 1898; Ellis 1931, 1936; Cordone and Kelly 1961; Imlay 1972; Coon et al. 1977; Marking and Bills 1979; Wilber 1983; Dennis 1985; Schuster et al. 1989; Wolcott and Neves 1991; Houp 1993; Richter et al. 1997, Brim Box 1999; Fraley and Ahlstedt 2001). Sources, biological effects, and the control of sediment in streams were reviewed by Cordone and Kelly (1961) and Waters (1995), while Mount (1995) provided an overview of the effects of various land uses on stream systems. Brim Box and Mossa (1999) reviewed how mussels are specifically affected by sediment and discussed land-use practices that may impact mussels.

Specific biological impacts on mussels from excessive sediment include reduced feeding and respiratory efficiency from clogged gills, disrupted metabolic processes, reduced growth rates, increased substrate instability, limited burrowing activity, and physical smothering (Ellis 1936, Stansbery 1971, Markings and Bills 1979, Kat 1982, Vannote and Minshall 1982, Aldridge et al. 1987, Waters 1995). Brim Box (1999) showed that burying adult mussels under 5.5 inches of sediment in the Apalachicola, Chattahoochee, and Flint River basin significantly decreased their chances of surviving. Intuitively, much thinner layers of sediment may result in juvenile mortality. Such studies tend to indicate that the primary impacts of excess sediment on mussels are sublethal, with detrimental effects not immediately apparent (Brim Box and Mossa 1999). The physical effects of sediment on mussels appear to be multifold (Brim Box and Mossa 1999). They are potentially impacted by changes in suspended and bed material load; bed sediment composition associated with increased sediment production and run-off in the watershed; channel changes in form, position, and degree of stability; changes in depth or the width/depth ratio, which affects light penetration and flow regime; actively aggrading (filling) or degrading (scouring) channels; and changes in channel position that may leave them high and dry (Vannote and Minshall 1982, Kanehl and Lyons 1992, Hartfield 1993, Brim Box and Mossa 1999; see earlier discussion on "Gravel Mining").

Interstitial spaces in mixed substrates may become clogged with sediment (Gordon et al. 1992). When clogged, interstitial flow rates and spaces may become reduced (Brim Box and Mossa 1999), thus reducing habitat for juvenile mussels and some adults as well. Interstitial spaces are relatively free of sediment in the Tennessee portion of the upper Clinch River, whereas upstream, at Pendleton Island in Scott County, Virginia, interstitial spaces were clogged with sediment (Butler, pers. obs., 1999). At the former site, small juvenile mussels were found in some abundance (oftentimes 4 to 6 inches deep in the substrate) but were generally lacking at Pendleton Island (Ahlstedt, unpublished data). Salomons et al. (1987) and the National Research Council (1992) indicated that sediment may act as a vector for delivering contaminants such as nutrients and pesticides to streams. Juveniles can readily ingest contaminants adsorbed to silt particles during normal feeding activities (see "Food Habits"). These factors may help explain, in part, why so many mussel populations appear to be experiencing recruitment failure.

Host fish/mussel interactions may be indirectly impacted by changes in stream sediment regimes through three mechanisms (Brim Box and Mossa 1999). First, fish abundance (Berkman and Rabeni 1987), diversity (Waters 1995), and reproduction (Muncy et al. 1979) may be reduced with increased sedimentation. Second, excessive sedimentation likely impedes host fish attractant mechanisms (e.g., mantle flaps, conglutinates, superconglutinates that mimic fish prey items; see "General Reproductive Biology of Mussels") (Haag et al. 1995, Burkhead et al. 1997). Third, sedimentation on shoal substrates may interfere with the ability of some species' adhesive conglutinates to adhere to rock particles (Hartfield and Hartfield 1996).

Many Southeastern streams have increased turbidity levels due to siltation (van der Schalie 1938). Some of these five species attract host fishes with visual cues, luring fish into perceiving that their glochidia are prey items (see "Reproductive Biology of the Five Species"). Such a reproductive strategy depends on clear water during the critical time of the year when mussels are releasing their glochidia (Hartfield and Hartfield 1996). Turbidity is a limiting factor impeding sight-feeding fishes (Burkhead and Jenkins 1991), and may have contributed to population declines in some of these species. In addition, mussels may be indirectly affected when turbidity levels significantly reduce the amount of light available for photosynthesis and the production of unionid food items (Kanehl and Lyons 1992).

Waterborne sediment is produced by the erosion of stream banks, channels, plowed fields, unpaved roads, roadside ditches, upland gullies, and other soil disturbance sites (Brim Box and Mossa 1999). This sediment results from poorly designed and executed agricultural and silvicultural activities; clearing of riparian vegetation for agricultural, silvicultural, construction, and flood control activities; gravel mining; and those developmental and other practices that allow erosion to occur, especially during storm-water discharges. The physical characteristics of stream channels are affected when large quantities of sediment are added or removed (Allan 1995, Waters 1995).

These changes include the formation of channel bars, erosion of banks, obstruction of flow, increase of flooding events, and shifting of the channel bottom.

Agricultural activities produce the most significant amount of sediment that enters streams (Waters 1995). Neves et al. (1997) stated that agriculture (including both sediment and chemical run-off) affects 72 percent of the impaired river miles in the country. Crop farming has been implicated in producing roughly 40 percent of the erosion in the United States (Meade et al. 1990), and 60 percent of the approximately 8,880 X 10^6 tons of soils lost annually from cropland is deposited in streams and reservoirs (U.S. Department of Agriculture [USDA] 1989). Reducing tillage not only reduces soil exposure, but it also reduces the nutrients and other contaminants that eroded soils carry into streams (National Research Council 1992). Despite the implications, only a few studies (e.g., Cooper 1987, Stewart and Swinford 1995) have specifically attributed changes in mussel populations to sediment derived from agricultural practices.

Armour et al. (1991) reviewed the effects of livestock grazing on riparian and stream ecosystems. Unrestricted access by livestock is a significant threat to streams (Trimble and Mendel 1995) and their mussel populations throughout much of the Cumberlandian Region (Anonymous 1999, Fraley and Ahlstedt 2001). Grazing may reduce infiltration rates and increase run-off and erosion (Brim Box and Mossa 1999). Trampling causes or accelerates stream-bank erosion, and grazing reduces a bank’s resistance to erosion (Armour et al. 1991, Trimble and Mendel 1995). In addition, livestock may add nutrients to streams at levels that are not easily assimilated, particularly during low-flow conditions, resulting in over-enrichment. Fraley and Ahlstedt (2001) attributed the decline of the Copper Creek mussel fauna between 1980 and 1998, among other factors, to an increase in cattle grazing and loss of riparian vegetation in the stream. They considered the oyster mussel and rough rabbitsfoot as possibly being extirpated from Copper Creek.

Erosion from silvicultural activities is more the result of logging roads than from the actual harvesting of timber (Waters 1995, Brim Box and Mossa 1999). Annual run-off and peak flow volumes increase with timber harvests, particularly during the wet season (Allan 1995). This is partially due to the construction of logging roads, and vegetation removal tends to compact soils, reduce infiltration rates, and increase soil erosion. Timber harvesting also results in stream channel changes (Brim Box and Mossa 1999) that may ultimately affect mussel beds.

Urban development changes sediment regimes by creating impervious surfaces and drainage system installations (Brim Box and Mossa 1999). The highest erosion rates are generally associated with construction activities, which can contribute sediment at a rate 300 times greater than from forested land (USDA 1977). Impervious surfaces reduce sediment input into streams, causing in-channel changes that may ultimately result in bank erosion and bed scouring (Brim Box and Mossa 1999). Stream channel erosion contributes up to two-thirds of the total sediment yield in urbanized watersheds (Trimble 1997).

Maintaining vegetated riparian buffers is a well-known method of reducing stream sedimentation and other run-off (Service 1980, Allan and Flecker 1993, Lenat and Crawford 1994). Buffers reduce impacts to fish and other aquatic faunas (Naiman et al. 1988, Osborne and Kovacic 1993, Belt and O'Laughlin 1994, Penczak 1995, Rabeni and Smale 1995) and are particularly crucial for mussels (Neves et al. 1997). A review of riparian buffer widths, extent, and vegetation, focusing on recent refereed scientific articles primarily in Georgia, was compiled by Wenger (1999). Schultz and Cruse (1992) evaluated their effectiveness as nutrient and sediment filters. Riparian forest removal in Southern Appalachian streams and subsequent sedimentation has been shown to be detrimental to fish communities (Burkhead et al. 1997, Jones et al. 1999). Particularly affected in the study by Jones et al. (1999) were benthic-dependent species (e.g., darters, benthic minnows, sculpins), which were found to decrease in abundance with longer deforested patches of riparian area. Benthic-dependent fishes, themselves disproportionately imperiled (Burkhead et al. 1997, Warren et al. 2000), commonly serve as hosts for numerous imperiled mussel species (Watters 1994), including four of the five mussels addressed in this recovery plan (see "Reproductive Biology of the Five Species").

Predation and Parasitism

The different life stages of mussels are preyed upon by a variety of invertebrate and vertebrate predators and infested by various parasites as part of natural ecosystem dynamics. Predators normally have minimal significant impacts upon the Cumberlandian Region fauna (Parmalee and Bogan 1998), with one potential exception. The muskrat (*Ondatra zibethicus*) has long been recognized in literature (e.g., Apgar 1887) as probably foremost among mussel predators. Muskrat predation upon rare mussels has been shown to be potentially detrimental to their recovery (Neves and Odom 1989). Apparently, it continues to be a significant, but seasonal and periodical, problem in localized stream reaches in at least the upper Tennessee River system (Koch, pers. comm. 1997). Although parasitism is not thought to be a significant problem in mussels (Parmalee and Bogan 1998), excessive trematode infestations in their gonads have been implicated in inducing mussel senescence (Zale and Neves 1982).

Alien Species

Alien species refers to those species "carried outside their original ranges by human activities" (Strayer 1999b). Invasions by alien aquatic species are a factor in streams throughout most of the continent. Impacts from alien species on mussels were reviewed by Neves et al. (1997) and Strayer (1997, 1999b).

The nonindigenous Asian clam was first reported from the Cumberlandian Region around 1959 (Sinclair and Isom 1961). This species has been implicated as a competitor with native mussels for resources such as food, nutrients, and space (Heard 1977, Kraemer 1979, Clarke 1986), particularly as juveniles (Neves and Widlak 1987). According to Strayer (1999b), dense populations of Asian clams may ingest large numbers of unionid sperm, glochidia, and newly metamorphosed juveniles. He also thought they actively disturb sediments, so dense populations may reduce habitable space for juvenile native mussels. Periodic dieoffs may produce enough ammonia and consume enough oxygen to kill native mussels (Strayer 1999b). However, specific impacts upon native mussels remain largely unresolved (Heard 1977; Leff et al. 1990; Strayer 1997, 1999b). Yeager et al. (2001) determined that high densities of Asian clams negatively impacted the survival and growth of newly metamorphosed juvenile mussels and thus reduced recruitment. They proved from laboratory experiments that Asian clams readily ingeted glochidia, clam density and juvenile mussel mortality were positively correlated, growth rates were reduced with the presence of clams, and juvenile mussels were displaced in greater numbers downstream in laboratory tests with clams. Yeager et al. (2001) presented the following summary:

> [a]fter eons of speciation and adaptation by native unionids . . . particularly in the Southeast, it is highly improbable that all available niches for bivalve filter-feeders [sic] were not filled by the native assemblage. There was no grand niche left vacant, such that the nonindigenous Asian clam could invade, achieve high densities, dominate in benthic biomass, and yet have no significant adverse effect on native unionids.

Densities of Asian clams are sometimes heavy in Cumberlandian Region streams, making competition with populations of some of these five species likely.

The invasion of the nonnative zebra mussel poses a threat to the mussel fauna of the Cumberlandian Region (Ricciardi et al. 1998). Zebra mussels in the Great Lakes have attached, in large numbers (up to 10,000 per unionid), to the shells of live and fresh dead native mussels (Schlosser and Kovalak 1991), and they have been implicated in the loss of mussel beds (Hunter and Bailey 1992, Masteller et al. 1993, Schlosser and Nalepa

1995). Although zebra mussels are now in the Tennessee and Cumberland River systems, the extent to which they will impact native mussels is unknown. However, as zebra mussels are likely to reach higher densities in the main stems, large tributaries, and below infested reservoirs, native mussels in these areas will likely be more heavily impacted than mussels in smaller streams without upstream reservoirs. Mussel extinctions are expected as a result of the continued spread of zebra mussels in the Eastern United States (Ricciardi et al. 1998).

Other potential threats from alien species on native mussels include the black carp (*Mylopharyngodon piceus*), a native of China (Strayer 1999b). Nico and Williams (1996) prepared a risk assessment of the black carp and summarized all known aspects of its ecology, life history, and intentional introduction (since the 1970s) into North America. A molluscivore (mollusk eater), the black carp has been proposed for widespread use by aquaculturists to control snails, the intermediate host of a trematode (flatworm) parasite affecting catfish in ponds in the Southeast. Another Asian carp species intentionally brought to the United States, they are known to eat clams (*Corbicula* spp.) and unionid mussels in China, in addition to snails. They are the largest of the Asiatic carp species, reaching more than 4 feet in length and achieving a weight in excess of 150 pounds (Nico and Williams 1996). The escape into the wild by nonsterile black carp is deemed imminent by conservation biologists (Mississippi Interstate Cooperative Resource Association 2000). If these species invade Cumberlandian Region streams, they could wreak havoc on already stressed native mussel populations.

The round goby (*Neogobius melanostomus*) is another alien invader fish species released in the 1980s into the Great Lakes in ballast waters originating in southeastern Europe (Strayer 1999b). They are well established in much of the Great Lakes, and will likely move south through the Mississippi River system as has the zebra mussel (Strayer 1999b). A voracious carnivore, despite its size (generally less than 10 inches in length), the round goby will eat native mollusks, zebra mussels, and small fishes that potentially serve as hosts for mussels. Round gobies also are aggressive competitors, and may eliminate or reduce populations of sculpins and darters (Strayer 1999b). The arrival of round gobies may therefore have important indirect effects on unionid communities through negative impacts to their host fishes.

Additional alien species will invariably become established in the United States in coming years, and will disrupt native species distributions and abundance (Strayer 1999b). These include *Limnoperna fortunei*, a freshwater mussel from southeast Asia that fouls solid objects as does the zebra mussel. This species has already spread to Japan and South America, and "probably will have strong effects" on native unionids (Strayer 1999b). Alien species may potentially carry with them diseases and parasites that may be devastating to the native biota. Because of our ignorance of mollusk diseases and parasites, "it is imprudent to conclude that alien diseases and parasites are unimportant" (Strayer 1999b).

Summary

Many of the impacts discussed above occurred in the past as unintended consequences of human development in the Cumberlandian Region. An improved understanding of these consequences has led to regulatory actions (e.g., the CWA); voluntary landowner measures (e.g., best management practices [BMPs] for agricultural, silvicultural, and construction activities); and improved land-use practices (e.g., maintaining riparian buffers, practicing no-till agriculture). These activities and others discussed under "Conservation Measures" are contributing to a reduction in threats to these mussels. Nonetheless, the five species are highly restricted in distribution, occur in generally small populations, and show little evidence of recovering from historic habitat losses without significant human intervention.

PATTERNS OF IMPERILMENT

The fate of freshwater mussel populations is influenced by a number of complex biological and ecological factors that are, in turn, ultimately affected by anthropogenic forces (Neves 1993). In addition, the elaborate life cycle of mussels increases the probability that weak links in their life history will preclude successful reproduction and recruitment. Following is an attempt to explain the consequences of the many factors that have contributed to the demise of mussel populations.

Reproductive Biology

Egg formation and fertilization are critical phases in the life history, as many mussels fail to form eggs (Downing et al. 1989), or fertilization is incomplete (Matteson 1948). Fertilization success has been shown to be strongly correlated with spatial aggregation, and either influences the rate of egg formation, or improves fertilization rates of individuals, or both (Downing et al. 1993).

A study of *Elliptio complanata* (Lightfoot 1786), in a Canadian lake (Downing et al. 1993) offers interesting insights on various aspects of reproductive biology. Complete fertilization failure occurred at densities of <0.9 mussels per square foot. Not until densities reached 3.7 per square foot were fertilization rates 100 percent. Thus, the fertilization success of sparse populations of species having separate species (i.e., nonhermaphroditic) is extremely low. Population viability is therefore questionable in mussel beds with low densities, and where fertilization does occur, recruits may be more homozygous than those in denser populations. Populations with cohort dominance skewed toward only old, large mussels will have limited reproductive success due to senescence. The occurrence of large numbers of gonad-destroying trematode parasites in old individuals of some mussel species (Zale and Neves 1982) might indicate senescence is partially a result of gonadal infestation.

The fluvial nature of riverine ecosystems would likely indicate that mussel beds would not need to be as aggregated for successful reproduction, as stream flow patterns would potentially disperse sperm over long linear distances. Where very low densities occur, however, reproductive success would probably be minimal. There is some evidence that hermaphroditism in certain mussel species may allow even minuscule populations to enjoy some level of reproductive viability (Neves, pers. comm., 1996). Hermaphroditism has not been investigated in these five species.

Host Fish Connection

Host fish availability and density are significant factors influencing where certain mussel populations can persist (Haag and Warren 1998). The apparently inefficient reproductive cycle involving obligate fish hosts would appear to be a weak link in population recruitment (Bogan 1993). Despite the high number of glochidia produced, contact between glochidia and host fishes is a low-probability event (Neves et al. 1997), promoted by the respiratory and feeding behavior of fishes (Dartnall and Walkey 1979, Neves et al. 1985) and the behavioral characteristics of some mussel species (Davenport and Warmuth 1965, Kraemer 1970). Infestation rates are therefore generally low for riverine mussels (Neves and Widlak 1988, Bruenderman and Neves 1993), but there are some exceptions (e.g., Michaelson and Neves 1995). Although glochidia may initially attach to many fish species, immune system incompatibility results in unsuitable fish hosts quickly sloughing off the parasites (Zale and Neves 1982).

Recruitment Failure

Despite the dearth of available quantitative information, the evidence is overwhelming that individual and combined stressors resulting from anthropogenic forces have been responsible for the demise of mussel faunas (Havlik and Marking 1987, Neves et al. 1997). Gradual reductions in recruitment and survival of vulnerable mussel species occur when anthropogenic factors act insidiously in altering sediment and water quality (Fleming et al. 1995).

Susceptibility of glochidia and host fish to altered and degraded habitats, coupled with the chance encounter between glochidia and host, can contribute to periodic recruitment failures (Zale and Neves 1982, McMurray et al. 1999a) and relic populations dominated by cohorts of older adults (Neves 1993, Stansbery 1995). Juveniles appear to be more susceptible to perturbations than adults (Ortmann 1909) and are hypothesized to be more susceptible to competitive interactions with the Asian clam for space or food (Neves and Widlak 1987). Lack of recent recruitment is apparent in many mussel populations (McMurray et al. 1999a, 1999b). It is possible that pedal-feeding juveniles that ingest contaminated sediment (see "Habitat Alteration") are precluding recruitment in some otherwise reproducing mussel populations. Unfortunately, many mussel populations are characterized by large, old, and spatially separated individuals that are commonly on their way toward extirpation (Stansbery 1995).

Mussel recolonization of impacted river reaches is achieved by dispersal of newly metamorphosed juveniles via infested host fish, passive adult movement downstream (Neves 1993), and active migration or passive movement downstream of juveniles (Kat 1982). Due to slow growth and relative immobility, however, the establishment of self-sustaining populations requires decades of immigration and recruitment, even where suitable habitat exists for common species that may occur in high densities (Neves 1993). Mussel recruitment is typically low and sporadic, with population stability and viability being maintained by numerous slow-growing cohorts and occasionally good year classes (Neves and Widlak 1987). Only when a significant number of viable populations have been verified should that species be considered stable (A. E. Bogan, North Carolina State Museum of Natural Sciences, in litt., 1995).

Due to their extreme longevity, direct effects of some anthropogenic factors on mussels may not be evident for years and, in some cases, not until the species has disappeared or experienced significant range reduction (Bogan, in litt., 1995). Studies suggest that although individual impacts may be minor, cumulative effects may become lethal over time (Bogan 1993).

Determination of the relative rarity of species has been divided by Rabinowitz et al. (1986) into the following three factors: (1) geographic range, (2) habitat specificity, and (3) population abundance. Based simply on the fact that these five species are highly restricted in range, are habitat specialists, and generally occur in small populations, their imperilment is made more acute.

Population Fragmentation and Genetic Considerations

Fragmentation of species' populations are the invariable result of many of the factors discussed under "Habitat Alteration." Page et al. (1997) reviewed the factors that contributed to population fragmentation and their impacts on midwestern aquatic organisms, while outlining management and restoration strategies that can mitigate fragmentation impacts. Neves (1997) presented a thorough summary of genetic considerations in freshwater mussel conservation.

Basic principles of population genetics give valuable insight into the heightened imperilment of rare species. Genomic heterogeneity is lost when the natural interchange of genetic material between populations is prohibited. Population genetics has emphasized the profound negative effects the loss of genomic heterogeneity has on the overall population viability of species with restricted and fragmented ranges (Chesser 1983, Gilpin and Soulé 1986). Such isolation can eventually lead to inbreeding depression (Avise and Hambrick 1996), which can be a major detriment to a species' recovery (Frankham 1995). Inbreeding may result in decreased fitness of multiple life stages, and the loss of genetic heterozygosity results in a significantly increased risk of extinction in localized natural populations (Saccheri et al. 1998).

The effect of heterozygosity on the extinction risk is most noticeable in small, isolated populations (Saccheri et al. 1998). However, even in populations exhibiting more intermediate levels of isolation, extinction risk increases dramatically with decreasing heterozygosity in the smallest populations. Unfortunately, according to Soulé (1980), it is likely that some of the extremely small and geographically isolated populations of these five mussel species may already be below their effective population size (EPS) or the level required to maintain long-term genetic viability (see "Narrative Outline," Recovery Task 1.3.6, for further discussion). The fragmentation of populations is of paramount importance when considering the likelihood of the long-term survival of narrowly distributed species (Burkhead 1993). The present fragmented distribution and imperiled status of most populations of these five species in the Cumberlandian Region may be indicative of the detrimental bottleneck effect resulting when the EPS is not attained.

Once-sizable populations of most of these species occurred throughout significant portions of the main stems of the large rivers and tributary systems comprising the Cumberlandian Region. This was particularly true for the Cumberlandian combshell and oyster mussel (see "Distributional History and Relative Abundance"). Historically, there were no natural absolute barriers to genetic interchange among their tributary subpopulations and those of their host fishes (with the notable exception of Cumberland Falls; see "Distributional History and Relative Abundance," Cumberland elktoe account).

With the completion of numerous dams on the main stems of the Tennessee and Cumberland Rivers and their large tributaries, primarily during the first half of the twentieth century, populations in long stream reaches were soon extirpated, effectively isolating the remaining populations. Small isolated tributary populations of imperiled short-lived species (e.g., most fishes) theoretically may have died out within a decade or so after, and as a direct result of, impoundment. This scenario is predicted by the hypothesis of disrupted source/sink populations (Pulliam 1988). Long-lived mussel species may potentially take decades for their populations to expire after impoundment, possibly longer if other factors were at play in their ultimate demise. This latter scenario is predicted by Levins' (1970) metapopulation model, in which reservoirs originally contributed to extirpations by disrupting the extinction/recolonization population dynamics. The date of extirpation in this model does not correlate with reservoir construction but rather with other detrimental factors.

Without the level of genetic interchange these species experienced historically (because of anthropogenic factors discussed in "Past and Present Threats"), many small isolated populations that are now comprised predominantly of adult specimens may be slowly dying out. This may, in part, account for the relatively recent demise of numerous tributary populations (see "Distributional History and Relative Abundance"). Even given the improbable absence of the impacts addressed in the "Past and Present Threats" section, we may lose smaller isolated populations of these species to the devastating consequences of below-threshold EPS (see "Narrative Outline" and Recovery Task 1.3.6 for further discussion). In reality, degradation of these isolated stream reaches, resulting in ever-decreasing patches of suitable habitat, is invariably contributing to the decline of the five species. Populations appear viable only where there are relatively large metapopulations in relatively extensive habitat patches (e.g., Cumberlandian combshell, oyster mussel, and rough rabbitsfoot in the upper Clinch River; Cumberland elktoe in the Big South Fork system).

Summary

In summary, mussels are jeopardized when their population size is diminished by any factor that reduces glochidial or juvenile survivability, adult spawning stocks, and host fish abundance (Neves 1993). Furthermore, any perturbation that limits fertilization rates and survivability of the glochidia; decreases host fish abundance; decreases fish community composition; and/or alters density, aggregation, or size distribution of mussel populations is detrimental to population viability and, ultimately, the species as a whole (Downing et al. 1993, Neves 1993, Neves et al. 1997). Many, if not all, of the factors addressed in this and the previous section have probably played, and some may continue to play, roles in the demise of the five mussels addressed in this recovery plan.

CONSERVATION MEASURES

Ecosystem management is the most effective method of protecting the greatest number of species (Doppelt et al. 1993, Shute et al. 1997). The Service, other governmental agencies, conservation organizations, and local watershed protection groups have implemented ecosystem management to conserve, restore, and recover Federal trust species and other rare aquatic species and their habitats nationwide. The Service has organized ecosystem teams, including the Southern Appalachian and Lower Tennessee/Cumberland Ecosystems in the range of these five species, to better manage each ecosystem's biota in a cross-program manner (Rappaport Clark 1999). This holistic approach to the management of biotic resources is deemed much more effective than managing single species in a complex natural and political environment. Shute et al. (1997) summarized the ecosystem approach to the management of imperiled aquatic resources, provided a literature review on the subject, and recommended a series of steps for developing and implementing an ecosystem management program. These include prioritizing ecosystems in need of protection, identifying and partnering with all potential agencies and organizations with watershed interests, prioritizing ecosystem threats, identifying strategies to minimize or eliminate threats, and educating ecosystem inhabitants and other stakeholders.

The Freshwater Mollusk Conservation Society was formed to conserve this highly imperiled fauna. Founding members of this organization and other individuals have published a national strategy to address mussel conservation (National Native Mussel Conservation Committee 1998). Its goals are to conserve native species; ensure their continued survival; and maintain their ecological, economic, and scientific values to our society (Neves 1997). Neves (1997) presents a summary of the national strategy and outlines actions needed to implement mussel conservation and recovery on a global scale.

Governmental Activities

A number of conservation measures are available for federally listed and other species pursuant to Federal and State regulations and other Federal and State activities. Wilcove and Bean (1994) reviewed existing legislation and other activities benefitting declining faunas of streams. They outlined ways in which legislation, water quality standards, dam operation modifications, creative incentives (e.g., market forces, tradeable discharge permits), and other proactive conservation measures may serve to preserve aquatic species such as jeopardized mussels.

Conservation actions by Federal, State, and private organizations, groups, and individuals are facilitated once a species has been listed under the Act. The Act requires that recovery actions be conducted for listed species; provides for possible land acquisition in cooperation with the States (Section 5); through cooperation with the States, provides funding to effect recovery activities (Section 6); requires Federal agencies to evaluate their actions with respect to any listed species (Section 7); and protects listed species from illegal taking (Sections 9, 10, and 11).

The CWA, administered by the EPA, has taken great strides in reducing point discharge pollutants into streams (Neves et al. 1997). Municipalities and industries have improved wastewater treatment facilities with grants and aid from the EPA and State environmental protection departments. Nonpoint-source pollution is dealt with in a number of ways under the CWA, including providing funds through its Section 319 nonpoint-source pollution program to improve water quality and reduce nutrient loading, sedimentation, and the likelihood of other pollutants entering streams. In addition, EPA and USGS have assessed and monitored water quality in streams throughout much of the Southeast.

Federal governmental involvement also includes the Fish and Wildlife Coordination Act (FWCA), which is intended to protect fish and wildlife resources and their habitats by coordinating with natural resource agencies on their projects. Programs under the USDA, particularly those administered by the Natural Resources Conservation Service (NRCS) (e.g., Conservation Reserve Enhancement Program [CREP], Environmental Quality Improvement Program, Wetland Reserve Program, Fish and Wildlife Habitat Improvement Program), are increasingly addressing restoration of impaired streams with imperiled species. For example, a proposed 10-year CREP project on the upper Green River system in Kentucky would earmark $110 million to farmers volunteering to take tens of thousands of riparian acres out of agricultural production, restoring habitat, and establishing conservation easements. The NRCS is routinely adopting animal waste management plans to reduce nutrient and sediment input into streams throughout the country.

The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 (NANPCA) was the first legislation authorizing the Service and the National Oceanic and Atmospheric Administration to issue regulations preventing the unintentional introduction of aquatic nuisance species. On February 2, 1999, the President issued Executive Order (EO) 13112 on invasive species. The EO places increased emphasis on efforts to prevent the introduction of invasive species; to provide for their control; and to minimize the economic, ecological, and human health impacts that invasive species cause. Regulations under the NANPCA and the EO will help prevent the incidental importation of other mollusks that are harmful to native species. The Service has developed four priorities under the title “Director’s Priorities FY 1999-2000.” One of the priorities is to develop and implement an aggressive program to enhance the Service’s capability and leadership role to respond effectively to present and future invasive species problems and issues. All Service offices and ecosystem teams will focus efforts via three goal statements--enhance leadership, take direct action, and raise public awareness.

Certain Cumberlandian Region streams, some of which harbor populations of these five species, receive a level of State protection by being designated as outstanding resource waters or are publicly owned and managed as wildlife management areas, parks, preserves, and historic areas. Some streams have been protected by the National Park Service. Much of the Big South Fork system, with populations of the Cumberland elktoe, oyster mussel, and Cumberlandian combshell, is protected as the Big South Fork National River and Recreation Area in northern Tennessee, as is a population of the purple bean in the Obed Wild and Scenic River in east-central Tennessee.

Priority Watersheds for Protection

Priority drainage regions in the United States based on numbers of at-risk fish and mussel species have been assessed by Master et al. (1998). The Cumberlandian Region easily ranks first of the 48 regions nationwide in this category, with 39 more at-risk species than the second place Mobile River basin (104 versus 65). Among smaller watersheds, Cumberlandian Region streams comprise 29 of 87 (33 percent) national drainages with the most significant imperiled aquatic resources, including 6 of the top 7. Numerous small drainages in the Cumberlandian Region with populations of multiple listed mussel species rank high for watershed-based restoration efforts. The current high quality conditions of many of the priority streams will facilitate the long-term protection and management of their imperiled mussel faunas. Regional watersheds that already have community-based restoration projects are listed in the next section.

Recently, TNC established a Freshwater Initiative with a Southern Rivers Director located in Chattanooga, Tennessee, to develop conservation strategies on focus streams in the multi-State area, based primarily on their study of critical watersheds for protecting biodiversity (Master et al. 1998). The World Wildlife Fund (WWF) recently completed a conservation assessment of freshwater ecosystems in North America (Abell et al. 2000). Both the WWF and American Rivers, another conservation organization promoting the welfare of rivers, have also stationed regional representatives in Chattanooga to work with partners in targeting high-biodiversity streams in the Southeast for protection and restoration.

Grassroots Support at the Watershed Level

Numerous stakeholders have realized that wise stream management, which involves restoring and protecting riparian habitat, improves water quality (Osborne and Kovacic 1993), enhances habitat for fishes (Belt and O'Laughlin 1994, Penczak 1995, Rabeni and Smale 1995), and is crucial for mussels (Neves et al. 1997). Numerous grassroots organizations have sprung up to initiate community-based watershed restoration projects in the region. These groups, consisting of local citizenry, band together to promote water quality and an awareness of aquatic habitat issues in their focus areas. In Alabama alone, the Alabama Rivers Alliance (ARA) has identified nearly 50 "grassroots watershed guardians" (ARA 1998). Similarly, more than 40 grassroots watershed-based groups have been identified in Kentucky (K. Wynne, Kentucky Waterways Alliance, pers. comm., 2000). These respective Alliances and their constituent watershed groups work at various levels to address a broad array of conservation issues. The importance of grassroots organizations cannot be overemphasized with regard to the conservation of riverine resources; their cooperation is invaluable.

The Service's Asheville, Cookeville, and Southwest Virginia Field Offices have partnered with a legion of stakeholders (e.g., TNC, NRCS, Resource Conservation and

Development Councils, State conservation agencies, grassroots watershed groups) to initiate several community-based riparian habitat restoration projects on streams having diverse mussel and other aquatic faunas within the Cumberlandian Region (Butler et al. 1999). Seed money, provided by the Service's Partners for Fish and Wildlife and Private Lands Incentives programs (each of which aids private landowners in restoring riparian habitat) and other sources, have been particularly instrumental in getting individual restoration programs started. TNC and other key partners have proved extraordinarily proficient at leveraging funds up to a ratio of 20:1 for on-the-ground projects and other related restoration and environmental outreach endeavors. The focus for these efforts is on agricultural watersheds, which are critical for the protection of water quality and aquatic life (Master et al. 1998). Projects include the Clinch/Powell, upper Holston, Little, Little Tennessee, Hiwassee, Sequatchie, Paint Rock, and Duck Rivers in the Tennessee River system and the Rockcastle River and Buck Creek in the Cumberland River system. Nearly all of these restoration projects are aiding in the recovery of the oyster mussel and/or Cumberlandian combshell, while the Clinch/Powell and upper Holston projects also benefit the purple bean and rough rabbitsfoot. In addition, the Rockcastle River project benefits the Cumberland elktoe. Other streams with populations of these species are being considered for future efforts (e.g., Big South Fork).

During the past decade, TNC has played a pivotal role in establishing and coordinating community-based restoration projects in the Cumberlandian Region. Demonstrating a strong commitment to imperiled aquatic resources, they have established bioreserves and other community-based projects on high-diversity streams, such as the upper Clinch River system in Tennessee and Virginia, Paint Rock River in Alabama and Tennessee, Duck River in Tennessee, and Horse Lick Creek/Rockcastle River and Buck Creek in Kentucky. The upper Clinch/Powell River, which has more at-risk mussel and fish species than any other small watershed, has also been selected by TNC as the highest priority watershed nationwide that is critical for protecting aquatic biodiversity (Master et al. 1998). The Kentucky Chapter of TNC is exploring the possibility of initiating a project in the Big South Fork, where as many as five listed species currently occur. Field representatives hired by TNC or the NRCS work closely with landowners and other stakeholders to effect riparian and aquatic habitat restoration. Partnering with State and Federal agencies and the coal industry, TNC is also working on the coal re-mining initiative, which addresses the complex issue of abandoned mine land (Master et al. 1998).

Riparian Habitat Restoration

The full protection of forested stream buffers is possibly the most important conservation action riparian landowners can take (Service 1980, Allan and Flecker 1993). A recent study of Southern Appalachian streams in a project watershed (Little Tennessee River, Macon County, North Carolina) concluded that forested buffers were absolutely critical for maintaining healthy benthic-dependent fish communities (Jones et al. 1999) and, conversely, mussel populations (Neves et al. 1997).

Restoration activities in priority watersheds conducted by community-based groups, TNC, and other stakeholders have helped improve riverine habitat in agricultural and other settings in many ways. Typical among these are reducing erosion by stabilizing stream banks and using no-till agricultural methods; controlling nutrient enrichment by carefully planning heavy livestock use areas; establishing buffer zones by erecting fencing and revegetating riparian areas; developing alternative water supplies for livestock; and implementing voluntary BMPs to control run-off for a variety of agricultural, silvicultural, and construction activities. BMPs vary from State to State, as does the level of participation by landowners. In order to increase their effectiveness in protecting aquatic resources, certain BMPs may need to be more stringent in order to minimize impacts to mussels and their habitats, and a higher level of landowner participation should be encouraged.

Despite their current level of imperilment, Neves (1999a) remains optimistic that nearly every stream with historically or currently significant mussel populations will become suitable for restoration if agricultural impacts are reduced. Perhaps the greatest accomplishment of all is that riparian landowners and other stakeholders are proving that they can be good stewards of the land by taking increased interest and pride in aquatic resources.

Propagation, Augmentation, and Reintroduction

Water and stream habitat quality improvements in parts of the Southeast have made it possible for mussel populations to expand in certain river reaches. Such improvements in habitat conditions have come to fruition through the concerted efforts of the Corps, TVA, EPA, and other Federal agencies; State water resource and natural resource agencies; industries; municipalities; conservation organizations; and concerned citizens. For instance, the TVA has modified water releases from several of its dams to improve water quality conditions in the tailwaters. Adjusting the thermal regime in the tailwaters of Cumberlandian Region dams would improve habitat and help promote reproduction for many federally listed mussels (Heinricher and Layzer 1999), including some of these five species.

State and Federal agencies and the scientific community have cooperatively developed mussel propagation and reintroduction techniques and conducted associated research that has facilitated the augmentation of extant populations and the reintroduction of mussels into historical and/or restored habitats (Watters 1994, Neves 1997, Garner 1999). A major reintroduction project is being planned for the Tennessee River at Muscle Shoals, Alabama, a site that was historically the most diverse of all known mussel beds worldwide (Ortmann 1924b, 1925; Stansbery 1964). The Service has published a proposed rule to designate experimental population status under Section 10(j) of the Act for the reintroduction of 16 federally listed mussel species and 1 aquatic snail to the remaining free-flowing habitat of the site below Wilson Dam, in the Tennessee River. Another area in the Holston and French Broad Rivers near Knoxville, Tennessee is currently under consideration for the reintroduction of 16 mussels (some of the same species). Furthermore, studies are underway to better understand and eliminate threats to mussels from contaminants, aquatic nuisance species, and other environmental perturbations, which could ultimately open up new areas for mussel translocation efforts.

Public Outreach and Environmental Education

Several Federal (e.g., U.S. Forest Service, NRCS, EPA, USGS, TVA, Corps) and other governmental agencies, conservation organizations, and grassroots groups have accomplished much in the field of public outreach and environmental education and should be commended for their collective achievements. Environmental education plays a major role in the Service's recovery and restoration programs in the Cumberlandian Region. Environmental education centers, pamphlets, stakeholder guides, and other outreach materials are common components of public outreach in project watersheds in many areas of the Southeast. Working with various other Federal agencies through a private company, an imperiled streams exhibit featuring mussels was recently installed in the Tennessee Aquarium in Chattanooga. "Aquatic trunks" represent a host of outreach materials that will enable secondary school educators to teach students about how the public benefits from aquatic ecosystems, while stressing the need for their protection and restoration. A large series of brochures, posters, and videos on mussels and fishes and other materials have been developed for public dissemination. Other projects being planned include *Russell the Mussel*, a storybook for children relating the plight of mussels, and a video on stream restoration techniques for private landowners.

PART II

RECOVERY

A. Recovery Objectives

The ultimate goal of this recovery plan is to restore viable populations[1] of the Cumberland elktoe (*Alasmidonta atropurpurea*), oyster mussel (*Epioblasma capsaeformis*), Cumberlandian combshell (*Epioblasma brevidens*), purple bean (*Villosa perpurpurea*), and rough rabbitsfoot (*Quadrula cylindrica strigillata*) to the point where they can be removed (through a regulatory action proposed and finalized through publication in the *Federal Register*) from the *Federal List of Endangered and Threatened Wildlife and Plants*. The number of secure viable stream populations (extant and restored) needed to achieve downlisting/delisting varies from species to species, depending on the extent of the species' historical range (i.e., species that were once widespread require a greater number of populations for recovery than species that were historically more restricted in distribution, regardless of the stream size they typically inhabit). A species can qualify for threatened status when it is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range or for endangered status when it is in danger of extinction throughout all or a significant portion of its range. The intent of recovery is to restore a species to the point where it no longer qualifies for either threatened or endangered status (i.e., restore a species to a significant portion of its range, remove

[1]**Viable population:** A wild, naturally reproducing population that is large enough to maintain sufficient genetic variation to enable the species to evolve and respond to natural habitat changes without further intervention. Viable populations will therefore have multiple age classes, including newly recruited juveniles. The demographic structure and effective population size of a viable population will be determined as Recovery Task 1.3.6.

the threats that would endanger the species, ensure that it is not in danger of extinction or of becoming an endangered species in the foreseeable future).

Recovery in the near future is not likely for the five species addressed in this plan because of the extent of their decline, the relative isolation of their remaining populations, their apparent sensitivity to common pollutants, and threats to their continued existence (see “Reasons for Decline”). This should not be construed as a failure of the Act or of conservation biologists charged with effecting their recovery. Doremus and Pagel (2001) argue that for many species permanent listing under the Act should be expected, since the primary protective measures are provided by the Act itself. Protecting their extant populations and occupied habitats, therefore, is the most immediate recovery priority for these species (see “Narrative Outline of Recovery Tasks, Task 1”). For most of these populations, protection can best be achieved at the watershed level by voluntary community stewardship awareness, action, planning, and other activities outlined under “Conservation Measures.”

Criteria for downlisting to threatened status:

The Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot will be considered for reclassification to threatened status when the likelihood of their becoming extinct in the foreseeable future has been eliminated by achieving the following criteria:

1. Through the protection of extant stream populations, reestablishment of historical stream populations, and/or discovery of currently unknown stream populations, there exists:

    a. At least eight distinct viable stream populations of the Cumberland elktoe in the Cumberland River system. This will be accomplished by:

(1) Protecting all extant stream populations (i.e., Laurel Fork, Marsh Creek, Sinking Creek, Big South Fork, Rock Creek, North White Oak Creek, Clear Fork, North Prong Clear Fork, Crooked Creek, Bone Camp Creek, White Oak Creek, New River) and ensuring that eight of these streams are recovered to viable population status.

b. At least seven distinct viable stream populations of the oyster mussel, including two in the Cumberland River system, three in the upper Tennessee River system,[2] and two in the lower Tennessee River system. This will be accomplished by:

(1) Protecting all extant stream populations (i.e., Clinch River, Powell River, Nolichucky River, Copper Creek in the upper Tennessee River system; Duck River in the lower Tennessee River system) and ensuring that the Clinch River and two other of these extant streams in the upper Tennessee River system and the Duck River in the lower Tennessee River system are recovered to viable population status.

(2) Designating nonessential experimental population status and reestablishing viable stream populations in the following streams: (a) two in the Cumberland River system (e.g., Rockcastle River, Big South Fork, Little South Fork, Buck Creek) and (b) one in the lower Tennessee River system (e.g., Paint Rock River, Elk River, Buffalo River, Tennessee River at Muscle Shoals, Shoal Creek)

c. At least seven distinct viable stream populations of the Cumberlandian combshell, including two in the Cumberland River system, three in the upper

[2]The dividing point between the upper and lower Tennessee River system is the Alabama/Tennessee State line near Chattanooga, Tennessee.

Tennessee River system, and two in the lower Tennessee River system. This will be accomplished by:

(1) Protecting all extant populations (i.e., Big South Fork, Buck Creek in the Cumberland River system; Clinch River, Powell River in the upper Tennessee River system; Bear Creek in the lower Tennessee River system) and ensuring that all of these streams are recovered to viable population status.

(2) Designating nonessential experimental population status and reestablishing a viable stream population in the upper Tennessee River system (e.g., upper Holston River/North Fork Holston River, lower Holston River, lower French Broad River) and one in the lower Tennessee River system (e.g., Paint Rock River, Elk River, Buffalo River, Tennessee River at Muscle Shoals, Shoal Creek).

d. At least three distinct viable stream populations of the purple bean in the upper Tennessee River system. This will be accomplished by:

(1) Protecting all extant stream populations (i.e., Clinch River, Indian Creek, Copper Creek, Obed River, Beech Creek) and ensuring that the Clinch River and two other of these extant streams are recovered to viable population status.

e. At least two distinct viable stream populations of the rough rabbitsfoot in the upper Tennessee River system. This will be accomplished by:

(1) Protecting all extant stream populations (i.e., Clinch River, Powell River, Indian Creek, Copper Creek) and ensuring that the Clinch River and one other of these extant streams are recovered to viable population status.

2. One distinct naturally reproduced year class exists within each of a species' viable stream populations. The year class must have been produced within 5 years prior to the time the species is reclassified from endangered to threatened. Within 1 year of the downlisting date, gravid females of the mussel and its host fish must be present in each viable population.

3. Studies of the mussels' biological and ecological requirements have been completed and any required recovery measures developed and implemented from these studies are beginning to be successful, as evidenced by an increase in population density and/or an increase in the length of the river reach inhabited by the species.

4. No foreseeable threats exist that would likely impact the survival of the species over a significant portion of their ranges.

5. Within larger streams (e.g., Big South Fork; Rockcastle, Clinch, Powell, upper Holston/North Fork Holston, Elk, Duck, Buffalo Rivers), the species is distributed over a long enough reach that a single catastrophic event is not likely to eliminate or significantly reduce the entire population in that stream.

6. Biennial monitoring of the five species (see "Recovery Task 6") yields the results outlined in "criterion 1" above over a 10-year period.

Criteria for removing the species from the *Federal List of Endangered and Threatened Wildlife and Plants*:

The Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot will be considered for removal from the *Federal List of Endangered and Threatened Wildlife and Plants* when the likelihood of their becoming endangered in the foreseeable future has been eliminated by achieving the following criteria:

1. Through the protection of extant stream populations, reestablishment of historical stream populations, and/or discovery of currently unknown stream populations, there exists:

   a. At least ten distinct viable stream populations of the Cumberland elktoe in the upper Cumberland River system. This will be accomplished by:

      (1) Protecting all extant stream populations (i.e., Laurel Fork, Marsh Creek, Sinking Creek, Big South Fork, Rock Creek, North White Oak Creek, Clear Fork, North Prong Clear Fork, Crooked Creek, Bone Camp Creek, White Oak Creek, New River) and ensuring that ten of these streams are recovered to viable population status.

   b. At least 11 distinct viable stream populations of the oyster mussel, including three in the Cumberland River system, five in the upper Tennessee River system, and three in the lower Tennessee River system. This will be accomplished by:

      (1) Protecting all extant stream populations (i.e., Clinch River, Copper Creek, Powell River, Nolichucky River in the upper Tennessee River system; Duck River in the lower Tennessee River system) and ensuring that all these populations are recovered to viable population status.

(2) Designating nonessential experimental population status and reestablishing viable stream populations in the following streams: (a) three in the Cumberland River system (e.g., Rockcastle River, Big South Fork, Little South Fork, Buck Creek); (b) one in the upper Tennessee River system (e.g., lower Holston River, upper Holston River/North Fork Holston River, lower French Broad River); and (c) two in the lower Tennessee River system (e.g., Paint Rock River, Elk River, Buffalo River, Tennessee River at Muscle Shoals, Shoal Creek).

c. At least 10 distinct viable stream populations of the Cumberlandian combshell, including three in the Cumberland River system, four in the upper Tennessee River system, and three in the lower Tennessee River system. This will be accomplished by:

(1) Protecting all extant stream populations (i.e., Big South Fork, Buck Creek in the Cumberland River system; Clinch River, Powell River in the upper Tennessee River system; Bear Creek, Duck River in the lower Tennessee River system) and ensuring that all these populations are recovered to viable population status.

(2) Designating nonessential experimental population status and reestablishing viable stream populations in the following streams: (a) one in the Cumberland River system (e.g., Rockcastle River, Little South Fork); (b) two in the upper Tennessee River system (i.e., lower Holston River, upper Holston River/North Fork Holston River, lower French Broad River); and (c) one in the lower Tennessee River system (e.g., Paint Rock River, Elk River, Shoal Creek, Tennessee River at Muscle Shoals, Buffalo River).

d. At least four distinct viable stream populations of the purple bean in the upper Tennessee River system. This will be accomplished by:

(1) Protecting all extant stream populations (i.e., Clinch River, Indian Creek, Copper Creek, Obed River, Beech Creek) and ensuring that the Clinch River and three of these other streams are recovered to viable population status.

e. At least three distinct viable stream populations of the rough rabbitsfoot in the upper Tennessee River system. This will be accomplished by:

(1) Protecting all extant stream populations (i.e., Clinch River, Powell River, Indian Creek, Copper Creek) and ensuring that the Clinch River and two of these other streams are recovered to viable population status.

2. Two distinct naturally reproduced year classes exist within each of the viable populations. Both year classes must have been produced within 10 years, and one year class must have been produced within 5 years of the recovery date. Within 1 year of the recovery date, gravid females of the mussel and its host fish must be present in each viable population.

3. Studies of the mussels' biological and ecological requirements have been completed and recovery measures developed and implemented from these studies have been successful, as evidenced by an increase in population density and/or an increase in the length of the river reach inhabited in each of the viable populations.

4. No foreseeable threats exist that would likely threaten the survival of any of the viable populations.

5. Within larger streams (e.g., Big South Fork; Rockcastle, Clinch, Powell, upper Holston/North Fork Holston, Elk, Duck, Buffalo Rivers), the species is distributed over a long enough reach that a single catastrophic event is not likely to eliminate or significantly reduce the entire population in that stream.

6. Biennial monitoring of the five species (see “Recovery Task 6”) yields the results outlined in “criterion 1” above over a 10-year period.

Listing/Recovery factor criteria:

The following criteria (Factors A through E) apply equally to downlisting endangered species and eventually delisting them. These criteria are linked to specific recovery tasks and serve to measure progress in removing threats to the species that is sufficient, in combination with the population criteria, for the Service to consider downlisting or delisting the species.

Factor A: The present or threatened destruction, modification, or curtailment of a species’ habitat or range. To provide assurance of population stability when any of the five species increase to the levels specified under the population criteria, threats to their habitat must be reduced as specified under this factor. Populations of the five species have declined in response to a wide variety of impacts upon streams and watersheds (see “Reasons for Decline, Habitat Alterations”). Therefore, reducing threats to their habitat must be accomplished through a broad application of measures for protecting water quality and quantity and through the restoration of stable natural stream channels and riparian zones as buffers from various developmental activities. Effective watershed conservation will not only serve to reduce habitat threats to the listed mussels but also will benefit all other native components of the aquatic ecosystem, including the host fish species essential for completing the mussels’ life cycles. The following criteria shall serve to indicate a reduction in habitat threats:

1. Water quality and quantity are fully supporting a designated use for fishing and for fish and wildlife habitat (as reported by the States under Section 305(b) of the CWA) in all streams where the five mussels occur. Give special consideration to "biocriteria" used in assessing water quality (e.g., Index of Biotic Integrity). Tasks 1.1, 2.1.1, 2.1.4, and 3.1 will contribute toward achieving this criterion.

2. Stream systems currently supporting populations of the five mussels and those needed for recovery are not further fragmented by new dams, water withdrawals, or other habitat alterations that may preclude the movement of host fish species between occupied sites. The stream systems that are listed above under "criterion 1" for downlisting and delisting are the areas the Service regards, for management purposes, as separate populations of the listed mussels. However, host fish species are not necessarily able to move between occupied sites within all of the stream systems due to impoundments and possibly other barriers. Any status surveys shall assess whether new barriers to fish passage have developed since listing that have genetically separated occupied sites within a stream system. Tasks 1.1, 2.1.1, 2.1.2, 2.1.3, 2.1.4, 3.1, 3.2.3, and 3.2.5 will contribute toward preventing such separation.

3. Stream channels at all sites occupied by the five mussels are stable (not actively aggrading or degrading or undergoing excessive bank erosion) and adjacent riparian zones are adequately vegetated. Task 4.1 will develop a protocol for assessing this listing/recovery criterion as part of rangewide status surveys that will collect data for the population criteria. Tasks 2.1.1, 2.1.2, 2.1.3, 3.2.3, and 3.2.5 will contribute toward achieving this criterion.

Listing/Recovery Factor B: Overutilization for commercial, recreational, scientific, or educational purposes. To provide assurance of population stability when any of the five species increase to the levels specified under the population criteria, overutilization for commercial, recreational, scientific, or educational purposes that threaten their continued existence must be reduced as specified under this factor. None of these five mussels have commercial value at the present time. The increasing rarity of these five species may make them more appealing to shell collectors. This potential threat is not considered to be a significant enough problem to alter the listing/recovery criteria outlined in this section. Therefore, at this time, overutilization for commercial, recreational, scientific, or educational purposes is not considered to be a limiting factor; thus, no reclassification (downlisting or delisting) criteria are necessary.

Listing/Recovery Factor C: Disease or predation. To provide assurance of population stability when any of the five species increase to the levels specified under the population criteria, disease or predation that threaten their continued existence must be reduced as specified under this factor. Disease has been suspected in mussel dieoffs in various streams. Predation by muskrats is a localized and sporadic problem with some mussels, occasionally including these five species. However, there is no data indicating that disease or predation are limiting factors; thus, no reclassification (downlisting or delisting) criteria are necessary.

Listing/Recovery Factor D: The inadequacy of existing regulatory mechanisms. To provide assurance of population stability when any of the five species increase to the levels specified under the population criteria, any inadequacy of existing regulatory mechanisms that threaten their continued existence must be reduced as specified under this factor. The final rule determining that these five mussels are endangered stated that existing authorities, such as the CWA, may not have been fully utilized in the protection of aquatic systems. In addition, current numerical criteria for pollutants such as ammonia may not be protective of mussels (Augspurger et al., in prep.). Task 1.1 will address these needs. Continuing research on other threats to these species may identify areas where existing regulatory mechanisms are inadequate for their protection. Tasks 1.3.3, 1.3.4, and 1.3.5 will address these concerns.

Listing/Recovery Factor E: Other natural or man-made factors affecting its continued existence. To provide assurance of population stability when any of the five species increase to the levels specified under the population criteria, several natural and man-made threats to their continued existence must be reduced as specified under this factor. These threats include the presence and potential introduction of nonindigenous species (especially the zebra mussel and black carp), insufficient densities of host fish species in streams supporting the five species, inbreeding depression and other genetic considerations, and possible weak links in the species' life cycles (see "Reasons for Decline, Patterns of Imperilment"). The following criteria shall serve to indicate a reduction in natural and other man-made threats: (1) zebra mussels, black carp, and other alien species not presently occurring in the region are not established in the stream systems supporting the five species; (2) relatively stable, nonimperiled populations of host fish species are present in each stream system; (3) genetic diversity is sufficient within each stream system; and (4) weak links in the life cycle of each species are identified and remedied through research, habitat improvement, propagation, translocation, or other means.

B. Narrative Outline

1. **Preserve extant populations and currently inhabited habitats.** Since only a small number of populations of these five species exist, it is essential that they all be protected.

   1.1 Continue to use existing legislation and regulations (e.g., the Act, CWA, FWCA, Federal and State surface mining laws, wetland and water quality regulations, stream alteration regulations, Federal Energy

Regulatory Commission relicensing) to protect the species and their habitats. Prior to and during implementation of this recovery plan, it is critical to the species' survival that Federal and State agencies continue to protect the extant populations with those laws and regulations that address protection and conservation of the species and their habitats. Where current numerical criteria of certain pollutants (e.g., ammonia, Augspurger et al., in prep; copper, Wilcove and Bean 1994) may not be protective of mussels, these standards should be adjusted to better conserve mussel resources.

1.2 **Solicit help in protecting the species and their essential habitats through the development of cooperative partnerships (e.g., community-based watershed restoration projects) with Federal and State agencies, local governments, agricultural groups, mining interests, conservation organizations, local landowners, and other stakeholders.** Section 7 consultation under the Act, the Fish and Wildlife Coordination Act, and other laws and regulations can assist in the protection of species when Federal programs are involved, but the implementation of these programs alone cannot recover the species. The assistance of various stakeholders, working at the ecosystem and watershed levels, will be essential for the conservation and restoration of imperiled mussel populations (Williams and Neves 1995; see "Conservation Measures"). More importantly, the support of the local community, including agricultural, silvicultural, mining, construction, and other developmental interests; local individuals; and landowners, will be essential in order to meet these recovery goals. Without a partnership with the people who live and work in these watersheds and who have an influence on habitat quality, recovery efforts will be doomed.

1.2.1 **Meet with local government officials and regional and local planners to inform them of our plans to attempt recovery for these**

species and request their support. This recovery criterion is particularly important in high-growth metropolitan areas in the Cumberlandian Region.

1.2.2 **Meet with agricultural, silvicultural, mining, construction, and other developmental interests and try to elicit their support in implementing protection and conservation actions.** The support of these groups is essential. They should be informed of current, but strictly voluntary, BMPs that could be implemented in order to minimize the impact of their activities on aquatic resources. Where they fail to adequately prevent significant impacts to mussels, BMPs should be made more stringent (see "Conservation Measures"). These interest groups should be encouraged to promote the safe mixing, application, storage, and disposal of pesticides, herbicides, and fertilizers and to comply with current water quality regulations. In addition, landowners should be encouraged to consider alternative pest management approaches that do not use synthetic pesticides.

1.2.3 **Develop cooperative ventures with private landowners to restore riparian habitat through programs like the Service's Partners for Fish and Wildlife Program and those administered by the USDA.** Federal and State natural resource agencies and conservation organizations, in cooperation with willing landowners, have begun to implement programs to restore riparian and aquatic habitat (see "Conservation Measures"). These programs, which are designed to benefit both the landowner and our natural resources, should be pursued with willing landowners to help minimize soil erosion and toxic run-off and enhance habitat for these five mussels.

1.3 Conduct life history studies and other research necessary for the species' management and recovery, determine threats, and implement management actions where needed. Neves (1999a) stated that probably the greatest hindrance to the recovery of imperiled mussels is more an issue of the biological traits of disjunct populations than it is of suitable habitat. Key biological factors (e.g., population isolation, low density, reproductive failure) are impeding any natural attempts of rare species to recover themselves. Garner (1999) presented an outline of research needs required for the conservation of Southeastern unionids.

1.3.1 Conduct life history research on the species to include such factors as reproduction, food habits, age and growth, and demography. Some limited information is available with regard to the life history of these species (see "Life History"). However, much additional life history information will be needed in order to successfully implement the recovery tasks.

1.3.2 Characterize the species' habitats (e.g., relevant physical, biological, and chemical components) for all life history stages. These species have been able to withstand some degree of habitat degradation. However, much of their habitat has been so severely altered that the species have been extirpated from numerous stream reaches (see "Distributional History and Relative Abundance"). Knowledge of species-specific microhabitat requirements and ecological associations is needed in order to focus management and recovery efforts on explicit habitat problems.

1.3.3 Determine present and foreseeable threats to the species. Impoundments, channelization, pollution, sedimentation, and other perturbations have contributed, and may continue to contribute, to substrate, water quality, and riparian zone degradation. The mechanisms by which the species and their habitats are impacted by these factors are poorly understood (Brim Box and Mossa 1999), and the extent to which the species can withstand these impacts is not known. In particular, the effects of these impacts upon juveniles, potentially the weakest link in their life cycle (see "Patterns of Imperilment"), should be investigated.

1.3.4 **Determine contaminant sensitivity for each life history stage.** Sensitivity of mussel glochidia, juveniles, and adults to common contaminants may vary significantly (see "Reasons for Decline"). The technology and methodology to determine sublethal and lethal levels of contaminants (e.g., pesticides, herbicides, and chemical discharges) on these species or their surrogates should be developed. The effects of multiple-toxin "cocktails" should be investigated for those compounds commonly encountered in Cumberlandian Region streams.

1.3.5 **Based on the biological data and threat analyses, investigate the need for management, including habitat improvement.** Additional management actions, where needed, should be implemented in order to secure viable populations of these species. Specific components of the species' habitats may be lacking, limiting the species' potential expansion, or certain activities in the watersheds may be adversely impacting the species. Habitat improvement programs will probably be needed as a prerequisite for mussel reintroduction into historical habitat and in order to increase host fish abundance, spawning success for both mussels and host fishes, and overall survivability. Cooperative projects with willing landowners for the purpose of providing alternative water sources may be needed to help minimize the impacts of water withdrawal and livestock access to the streams (see Task 1.2.3). Such efforts will be needed to overcome some of the threats identified in Task 1.3.3.

1.3.6 **Determine the number of individuals and the sex ratio required to maintain long-term viable natural populations.** Inbreeding depression can be a major obstacle to a species' recovery, especially if the remaining population size is small and/or has gone through some type of genetic bottleneck (Neil et al. 1975, Avise and Hambrick 1996). The actual number of individuals in a population is not necessarily a good indication of a population's genetic viability; rather, the EPS is critical (Neves 1997, Garner 1999). The EPS is the size of an "ideal" population in which genetic drift takes place at the same rate as in the actual population (Chambers 1983).

Franklin (1980) suggested that the inbreeding coefficient should be limited to no more than 1 percent per generation, a figure which implies that maintenance EPS, in the short term, should be no fewer than 50 individuals (Franklin 1980, Soulé 1980, Frankel and Soulé 1981). Because the EPS is typically only one-third to one-fourth the actual population size (being affected by sex ratio, overlapping generations, generally nonrandom distribution of offspring, and nonrandom mating) (Soulé 1980), a population of 150 to 200 individuals is needed for short-term population maintenance. Soulé (1980) further suggests that for long-term viability, an EPS of 500 individuals is necessary, translating into a population size of 1,500 to 2,000 individuals.

The EPS, adequate density within populations, and sex ratios for these five mussel species needs to be determined in order to calculate whether their remaining populations are capable of long-term self-maintenance or whether propagation and augmentation programs should be initiated. Allozyme and/or mitochondrial DNA studies should also be considered in order to assess genetic variability and viability in the remaining populations of the five species.

1.3.7 **Conduct detailed anatomical and molecular genetic analyses of the five species throughout their ranges.** Researchers in the Southeastern United States recognize that the taxonomic identity for many mussel taxa has probably not been determined (Butler 1989, Mulvey et al. 1997) and that this information is crucial to mussel conservation (Williams and Mulvey 1997, Lydeard and Roe 1998, Roe 2001). There is evidence that the oyster mussel may represent a species complex (see "Species Descriptions"). If true, the taxa that comprise this complex are more endangered than the oyster mussel. Accordingly, there would be major implications for the recovery and management of the multiple entities comprising the species complex. Research on molecular genetics, soft anatomy, life history, and ecology should be undertaken to determine if the oyster mussel or any population of the other four species is a distinct genetic entity that may warrant specific conservation and management consideration. Genetic information (e.g., allozyme or mitochondrial DNA studies) on various populations of these species would also be useful in determining which genetic stocks should be used in particular translocation efforts (see Task 3). Otherwise, there is the risk of inadvertent genetic swamping of species via introgressive hybridization or loss of populations from outbreeding depression (Avise and Hambrick 1996, Lydeard and Roe 1998).

2. **Develop a prioritized list, by species, of streams and stream reaches that should be surveyed.** A prioritized list of streams in need of surveying would help determine where limited survey funds should be spent.

   2.1 **Search for additional populations of the species and suitable habitat.** It is possible that some currently unknown populations of these five species may exist. An effort should be made to search unsurveyed river reaches and to resurvey river reaches from which the species are thought to have disappeared.

3. **Determine, through research and propagation technology, the feasibility of augmenting extant populations and reintroducing the species into historical habitat.** Mussel propagation technology and subsequent translocation are fast becoming important tools in the recovery of native populations (Garner 1999). See Neves (1997) for a summary of captive propagation and mussel translocations and Watters (1994) for an annotated bibliography of mussel propagation studies. Severe range restriction and overall population declines characterize the status of these species. Their recovery is not possible without augmenting some extant populations and/or reintroducing populations into habitat within their historical ranges.

   3.1 **Refine techniques and methodologies for propagating and translocating individuals as a prelude to potential augmentation and reintroduction efforts.** Sufficient specimens of most listed mussels are not presently available to allow for the translocation of enough adults to augment or reintroduce populations. These methodologies will need to be tested on a variety of species in order to increase production levels and improve survival rates of captive-propagated and translocated animals.

3.2 Determine the need, appropriateness, and feasibility of augmenting and expanding certain extant populations. Many extant populations may be characterized by a size or demographic composition that is insufficient to maintain long-term genetic viability (see Task 1.3.6 and "Reasons for Decline"). These populations may be able to expand naturally if environmental conditions are improved. However, some populations may be too small and may need to be augmented to reach a sustained level of viability.

3.2.1 In coordination with partners, survey efforts should be undertaken to identify and prioritize extant populations as a prerequisite for augmentation activities based on biological, ecological, and habitat characterization criteria. A set of biological, ecological, and habitat parameters will need to be developed to determine if an extant population will be suitable for species augmentation. Prioritized populations for this task will be selected based on present population size, demographic composition, population trend data, potential site threats, habitat suitability, and any other limiting factors that might decrease the likelihood of long-term benefits from population augmentation efforts.

3.3 Determine the need, appropriateness, and feasibility of reintroducing the species into prioritized stream reaches within their historical ranges. Numerous populations of these five species have been lost from streams and stream reaches within their historical ranges (see "Distributional History and Abundance"). Habitat and water quality improvements have recently been documented in some stream reaches where these species once occurred (see "Conservation Measures"). However, since extant populations are isolated by impoundment or otherwise long stretches of inappropriate habitat, natural repopulation of now suitable but unoccupied historical habitat is impossible.

This task will explore the possibility or reintroducing populations into unoccupied historical habitat.

3.3.1 In coordination with partners, survey efforts should be undertaken to identify and prioritize sites within the species' historical ranges as a prerequisite for reintroduction activities based on biological, ecological, and habitat characterization criteria. A set of biological, ecological, and habitat characterization parameters will need to be developed to determine if a site will be suitable for species reintroduction. These will include habitat suitability, substrate stability, presence of host fishes, potential site threats, and any other limiting factors that might decrease the likelihood of long-term benefits from population reintroduction efforts.

3.4 Identify and prioritize those streams, stream reaches, and watersheds most in need of habitat recovery and protection from further threats to these species and their host fishes. Streams, stream reaches, and watersheds should be prioritized for protection based on a variety of factors, with emphasis on conserving the best existing habitats and stream reaches as opposed to restoring habitats. These factors include high endemicity; high diversity of imperiled species; biogeographic history of rare species; highly fragmented habitats; cost effectiveness and ease of preservation, management, recovery, and restoration; landowner complexity; watershed size; existing land-use patterns; public accessability; likelihood for success; and those systems exhibiting low resilience to disturbance (Angermeier et al. 1993, Carroll and Meffe 1994, Shute et al. 1997). Furthermore, augmentation and reintroduction activities should not be conducted at totally unprotected sites or at sites with significant uncontrollable threats.

3.5 **Augment extant populations and/or establish new populations within their historical ranges.** Using the techniques developed under Task 3.1, activities to augment and/or establish populations of the five species should be undertaken.

3.6 **Implement protective measures for reintroduced populations.** Although reintroduced populations will undoubtably be designated nonessential experimental populations and will not receive the full protection of Sections 7 and 10 of the Act, other laws and regulations can provide protection for these populations.

4. **Develop and implement a program to evaluate efforts and monitor population levels and habitat conditions and assess the long-term viability of extant, newly discovered, augmented, and reintroduced populations.** During and after the implementation of recovery actions, the program should be evaluated, and the status of the species and their habitats must be monitored to assess progress toward recovery. Information gathered from this task and Task 3.1 will aid in refining techniques and methodologies that are critical aspects of the recovery program for these species. Stream reaches with augmented and/or reintroduced populations should be monitored biannually for at least 10 years to evaluate the success of these activities.

4.1 **Develop a comprehensive Geographic Information System (GIS) database to incorporate information on the species' distribution, population demographics, and various threats identified during monitoring activities.** A GIS database will act as a tool to do the bookkeeping for the population criteria and, to the extent practicable, for the listing/recovery factor criteria as well.

5. **Develop and implement cryogenic preservation techniques to preserve the species' genetic material until such time as conditions are suitable for reintroduction.** Cryogenic preservation of the species could maintain genetic material (much like seed banks for endangered plants) from all extant populations. If a population were lost to a catastrophic event, such as a toxic chemical spill, cryogenic preservation could allow for the eventual reestablishment of the population using the genetic material preserved from that population.

6. **Develop and utilize a public outreach and environmental education program.** A comprehensive outreach and environmental education program is an important part of the recovery process.

   6.1 **Develop a public outreach and environmental education program to promote an aquatic ecosystem management and community-based watershed restoration approach to managing water and aquatic habitat quality in the Cumberlandian Region.** The use of tools and activities (e.g., slide/video presentations, workshops, volunteer workdays, mobile displays, brochures) to achieve this task should be championed among law enforcement personnel; conservation organizations; governmental agencies; schools; agricultural, silvicultural, and developmental groups; civic and youth groups; churches; and other watershed stakeholders. Educational materials and activities that further recovery goals, with emphasis on the ecological and human benefits to be derived from maintaining and upgrading water and aquatic habitat quality, is essential for gaining public support for this recovery program and fostering pride in, and the wise stewardship of, these natural resources.

7. **Annually assess the overall success of the recovery program and recommend action (e.g., changes in recovery objectives, delist, implement new measures,**

conduct additional studies). The recovery plan must be evaluated periodically to determine if it is on track and to recommend future actions. As more is learned about these species, the recovery objectives may need to be modified.

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D. Glossary

Allopatric: Pertaining to populations of two or more species whose ranges do not occupy the same geographical area.

Anthropogenic: Activities involving the impact of man on nature.

Bioreserve: A discreet geographic region, such as a watershed, that has been established by a conservation organization as a focus area for habitat restoration and other concerted conservation efforts.

Byssus: A protein thread secreted by juvenile mussels as a means of attachment to hard surfaces; byssal thread.

Cohort: All the organisms produced in a single breeding season; year class.

Contra: Latin for against. Herein used in reference to a published finding that is contradictory to that previously published (e.g., *contra* Lydeard et al. 1999).

Distinct Viable Population: A population that satisfies the criteria specified in the February 7, 1996, *Federal Register*, pages 4722-4725. The criteria require it to be readily separable from the rest of its populations and to be biologically and ecologically significant. Such a population responds to natural habitat changes without any intervention. Also see "viable population."

Endemic: Native or confined to a certain region and having a relatively restricted distribution.

Extant: Currently existing populations of species.

Genetic Bottleneck: When the number of breeding specimens in a population is reduced to a level that results in the loss of genetic variation as a consequence of decreased random genetic drift.

Geomorphic: Relating to earth, its shape, or surface configuration. Herein used in reference to stream channel morphology.

Glochidia, Glochidium: The bivalve larvae of freshwater mussels in the superfamily Unionoidea which are generally parasitic upon vertebrates, typically fish.

Hermaphrodyte: A sexual condition where male and female reproductive tissues are found in the same specimen.

Holotype: The single specimen chosen for designation of a new species and housed in a museum.

Lanceolate: Pointed or lance-shaped

Lateral Teeth: The elongated, raised, and interlocking structures located dorsally along the hinge line of the inside of the valves of mussels.

Marsupia: The portion of the gills of a female mussel that are used to incubate glochidia.

Metapopulation: Several populations that have the potential for natural genetic interchange.

Midden: A collection of discarded mussel shells harvested for food by Native Americans or muskrats.

Nacre: The interior iridescent, thin layer of a mussel shell; mother of pearl.

Neotype: The single specimen designated as a replacement when no other type specimen is thought to exist.

Nonindigenous: Organisms that are intentionally imported or accidentally introduced from another or foreign area; exotic or nonnative.

Periostracum: Exterior or outside protein-comprised layer of the shell.

Phagotrophic: The act of an organism ingesting or engulfing solid particles of food.

Phytoplankton: The plant organisms comprising plankton.

Piscivorous: Organisms that habitually feed on fish.

Pseudocardinal Teeth: Triangular-shaped hinge teeth near the anterior-dorsal margin of the inside of the valves.

Riverine: Found in or characteristic of rivers.

Sympatric: Pertaining to populations of two or more species which occupy identical or broadly overlapping geographical areas.

Translocation: A management tool that involves the movement of organisms from one location to another.

Type Locality: The locality from where the holotype for a newly described species was collected.

Umbo, Umbonal: The raised, inflated area of the bivalve shell, centrally or anteriorly placed along the dorsal margin of the valve. The oldest portion of the shell.

Unionid: Freshwater bivalve mollusks that belong to the superfamily Unionoidea, family Unionidae.

Valve: The left or right half of a bivalve shell, such as a mussel.

Viable Population: A wild, naturally reproducing population that is large enough to maintain sufficient genetic variation to enable the species to evolve and respond to natural habitat changes without further intervention. Viable populations will therefore have multiple age classes, including newly recruited juveniles.

PART III

TABLES AND FIGURE

Table 1. ***Alasmidonta atropurpurea*** **occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.**

Stream, County, State	Authority	Date
Cumberland River System		
Laurel Fork, Whitley County, KY	Cicerello and Laudermilk (2001)	1996, 1993
Cumberland River, McCreary and Whitley Counties, KY	Schuster (1988) Clarke (1981)	1935 ?
Laurel River, Laurel County, KY[1]	R. R. Cicerello (Kentucky State Nature Preserves Commission, personal communication [pers. comm.], 1997)	1948
Lynn Camp Creek, Whitley County, KY	Clarke (1981)	?
Marsh Creek, McCreary County, KY	Cicerello (in press) Call and Parmalee (1982)	1994 1979-80
Sinking Creek, Laurel County, KY	Cicerello (pers. comm., 1997)	1999
Big South Fork, Pulaski County, KY	Clarke (1981)	?
Big South Fork, McCreary County, KY	Bakaletz (1991)	1986
Rock Creek, McCreary County, KY	Cicerello (1996) D. H. Stansbery (Ohio State University Museum of Zoology, pers. comm., 1998) Call and Parmalee (1982)	1995 1987 1979
Big South Fork, Scott County, TN	S. A. Ahlstedt (U.S. Geological Survey, pers. comm., 1999) P. W. Shute (Tennessee Valley Authority, pers. comm., 1998) Bakaletz (1991) Hatcher and Ahlstedt (1982)	2000, 1998 1996 1986 1980
North White Oak Creek, Fentress County, TN	Ahlstedt (pers. comm., 1999)	1998-99
Clear Fork, Scott County, TN	Bakaletz (1991) Hatcher and Ahlstedt (1982)	1986 1980
Clear Fork, Fentress and Morgan Counties, TN [Type Locality][2, 3]	Gordon and Layzer (1993) Bakaletz (1991) Call and Parmalee (1982) Clarke (1981)	1988-89 1985-86 1980 <1897[4]
North Prong Clear Fork, Fentress County, TN	Gordon and Layzer (1993)	1988-89
Crooked Creek, Fentress County, TN	Ahlstedt (pers. comm., 2002)	2001

Stream, County, State	Authority	Date
White Oak Creek, Morgan County, TN	Call and Parmalee (1982)	1980
White Oak Creek, Scott County, TN	Bakaletz (1991)	1986
Bone Camp Creek, Morgan County, TN	Gordon and Layzer (1993)	1988-89
New River, Scott County, TN	Ahlstedt (pers. comm., 2002) Gordon (1991)	2002 <1991

[1]This museum record for *Strophitus rugosus* (=*Strophitus undulatus* [Say 1817]) by Neel and Allen (1964) actually represents, in part, *Alasmidonta atropurpurea*.

[2]Clarke (1981:71) in his "Remarks" section of the *Alasmidonta atropurpurea* species account designated a neotype (U.S. National Museum of Natural History [USNM] 150522) for this species (Rafinesque's type material is lost), giving the locality as "South Fork, Cumberland River, Fentress Co., Tennessee collected by B. H. Wright." The South Fork does not flow through Fentress County, but a tributary, Clear Fork, does (forming the Fentress/Morgan County line), which better coincides with a locality Clarke (1981:71) presented in his "Geographical Records," "South Fork Cumberland River, Armathwaite, Fentress County, Tenn." (despite naming "J. Lewis! [Museum of Comparative Zoology (MCZ)]" and not "B. H. Wright! [USNM]" as the alleged collector and the museum of deposition, respectively, for this record). As further evidence on the clarification of this matter, Wright (1898) mentions a collection from "A branch of the South Fork of the Cumberland River at Armathwaite, Fentress Co., Tenn." of *Margaritana raveneliana* (=*Alasmidonta raveneliana* [Lea 1834]), actually *Alasmidonta atropurpurea*. In reality, this collection was made by Mr. E. F. Hassler, not Wright. This collection undoubtably refers to the Clear Fork site and represents the material upon which Clarke (1981) designated the neotype for *Alasmidonta atropurpurea*. The correct type locality should therefore read "Clear Fork, near Armathwaite and Rugby, Fentress/Morgan Counties, Tennessee," probably in the vicinity of the Tennessee Highway 52 crossing (see Footnote 3 below).

[3]In the *Alasmidonta marginata* account's "Geographical Records," under "Clinch River Drainage," Clarke (1981:66) reports "Clear Fork Creek, Rugby, Morgan Co. Tenn. (MCZ)." This record is probably for *A. atropurpurea* and presumably refers to the Clear Fork site in the Big South Fork system from which he designated the neotype for *A. atropurpurea* (see Footnote 2 above). Rugby (Morgan County) is approximately 5 miles from Armathwaite (Fentress County) on Tennessee Highway 52, with the Clear Fork crossing approximately halfway between the two towns.

[4]Clarke (1981:71) mentions that this collection of four specimens attributed to B. H. Wright (and from which the neotype was selected; see Footnote 2 above) was originally cataloged as USNM 783317 in January 1897.

NOTE: Other erroneous localities (see Footnote 2 above) are given for *Alasmidonta atropurpurea* by Clarke (1981): (1) the "North Fork Cumberland River (B. H. Wright! [USNM])" record given under "Geographical Records" is presumed to be from the main stem of the Cumberland River in Kentucky, as there is no North Fork Cumberland River; (2) his caption for the neotype (USNM 150522) illustrated in Figure 22 (p. 69) as being from the "Cumberland River, Tennessee," is actually the same locality for the neotype (Clear Fork) as stated under his "Remarks" section (p. 71; see Footnote 2 above); and (3) the locality given in Table 15, "South Fork, Cumberland River, Fentress County, Tennessee (University of Michigan Museum of Zoology 11190)" also represents the Clear Fork type locality (see Footnote 2 above). A record from Horse Lick Creek, Jackson County, Kentucky (Ahlstedt 1986), ". . . could represent a misidentification" of *A. marginata* (Cicerello et al. 1991). Accordingly, when the unpublished report record of Ahlstedt (1986) was published (Ahlstedt and Saylor 1995-96), the record was changed to *A. marginata*. Interestingly, *A. atropurpurea* has now been verified from the Rockcastle River system (Cicerello, in press), but it occurs much further downstream (Sinking Creek) from Horse Lick Creek. A

1978 *A. atropurpurea* record for Collins River, Grundy County, Tennessee, given by Call and Parmalee (1982) was considered a misidentification of *A. marginata* by Gordon (1995) or possibly represents an undescribed taxon (R. M. Anderson, USGS, pers. comm., 1998).

CODES: < = collected prior to (date).

Table 2. ***Epioblasma capsaeformis*** **occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.**

Stream, County, State	Authority	Date
Cumberland River System		
Cumberland River, McCreary and Whitley Counties, KY	Neel and Allen (1964)	1947-49
Rockcastle River, Laurel and Pulaski Counties, KY	Neel and Allen (1964)	1948
Cumberland River, Pulaski County, KY	R. R. Cicerello (Kentucky State Nature Preserves Commission, personal communication [pers. comm.], 1997)	?
Buck Creek, Pulaski County, KY	Schuster et al. (1989) Gordon (1991) H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997)	1984, 1982 1980-81, 1974-75, 1971 1959
Big South Fork, Scott County, TN[1]	S. A. Ahlstedt (U.S. Geological Survey, pers. comm., 1997) Bakaletz (1991)	1998 1986
Big South Fork, McCreary County, KY[1]	Gordon (1991) Bakaletz (1991) Schuster (1988) Harker et al. (1980)	~1990 1986 1986 1979
Big South Fork, Pulaski and Wayne Counties, KY	Neel and Allen (1964) Wilson and Clark (1914)	1948 1910-12
Cumberland River, Wayne County, KY	Wilson and Clark (1914)	1910-12
Cumberland River, Russell County, KY	Neel and Allen (1964) Wilson and Clark (1914)	1947 1910-12
Beaver Creek, Russell County, KY	Neel and Allen (1964)	1947-48
Cumberland River, Clinton County, KY	Wilson and Clark (1914)	1911
Cumberland River, Cumberland County, KY	Neel and Allen (1964)	1947
Obey River, Pickett County, TN	Gordon (1991) Johnson (1978)	1911 ?
Cumberland River, Smith County, TN	Parmalee et al. (1980)	A
Cumberland River, Davidson County, TN [Type Locality?]	Ortmann (1924a)	<1834?

Stream, County, State	Authority	Date
Harpeth River, Williamson County, TN	Athearn (pers. comm., 1997) Johnson (1978)	1964 ?
Harpeth River, Davidson County, TN	Pilsbry and Rhoads (1896) Johnson (1978)	1895 ?
Cumberland River, Stewart County, TN	P. W. Parmalee (University of Tennessee, pers. comm., 1997)	A
Tennessee River System		
Clinch River, Tazewell County, VA	Church (1991) Gordon (1991) Goodrich (1913) Ortmann (1918)	1989-90 1965 1913 1912-13
Clinch River, Russell County, VA	Gordon (1991) P. W. Shute (Tennessee Valley Authority, pers. comm., 1998) Athearn (pers. comm., 1997) Goodrich (1913) Ortmann (1918)	1985, 1963 1980 1967 1913 1913, 1899
Clinch River, Wise County, VA	Gordon (1991) Goodrich (1913) Ortmann (1918)	1965, 1963 1913 1912-13, 1899
Clinch River, Scott County, VA	L. M. Koch (U.S. Fish and Wildlife Service [Service], pers. comm., 1997) Ahlstedt and Tuberville (1997) Gordon (1991) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997) Ortmann (1918) Boepple and Coker (1912)	1997 1994, 1983, 1979 1990, 1970, 1963, 1944 1978-83 1973-75 1968-69, 1955, 1953 1913, 1899 1909
Little River, Russell County, VA	Shute (pers. comm., 1998)	1989 R
Copper Creek, Scott County, VA	Ahlstedt (pers. comm., 1997) Barr et al. (1993-94) Ahlstedt (1982) Gordon (1991)	1995, 1991 1981 1980 1970, 1965
Clinch River, Hancock County, TN	R. G. Biggins (Service, personal observation) Ahlstedt and Tuberville (1997) Barr et al. (1993-94 Ahlstedt (1991a) Dennis (1985) Gordon (1991) Ortmann (1918)	2000 1994, 1988, 1979 1981 1978-83 1973-75 1967 1899

Stream, County, State	Authority	Date
Clinch River, Claiborne and Grainger Counties, TN	Gordon (1991) Athearn (pers. comm., 1997) Ortmann (1918) Boepple and Coker (1912)	1968, 1965 1956, 1949 1915, 1913 1909
Clinch River, Union County, TN	Ortmann (1918) Boepple and Coker (1912)	1915, 1899 1909
Clinch River, Anderson County, TN	Hickman (1937) Cahn (1936b) Ortmann (1918)	1935-37 1936 1914-15
Powell River, Lee County, VA	Wolcott and Neves (1991) Wolcott and Neves (1994) Ahlstedt (pers. comm. 1997)[3] Barr et al. (1993-94) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997)	1989 1988-89 1983, 1979 1981 1979 1975-78 1973-78 1951
Wallen Creek, Lee County, VA[4]	Gordon (1991)	?
Powell River, Hancock County, TN	Barr et al. (1993-94) Ahlstedt (1991b) Ahlstedt and Tuberville (1997) Ahlstedt and Brown (1980) Dennis (1981)	1981 1979 1979 1975-78 1973-78
Powell River, Claiborne County, TN	Ahlstedt and Tuberville (1997) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997) Ortmann (1918)	1979 1979 1975-78 1973-78 1964 1915, 1913, 1899
Powell River, Campbell and Union Counties, TN	Ortmann (1918)	1899
Clinch River, Anderson and Knox Counties, TN	Ortmann (1918) Parmalee and Bogan (1986)	1914 A
Poplar Creek, Roane County?, TN	Gordon (1991)	?
North Fork Holston River, Washington County, VA	Ahlstedt (1980) Ortmann (1918)	1975 T 1900
North Fork Holston River, Scott County, VA	Neves (1995) Ahlstedt (1980) Ortmann (1918) Boepple and Coker (1912)	1991-95 R 1978, 1976 T 1913, 1901 1909

Stream, County, State	Authority	Date
North Fork Holston River, Hawkins and Sullivan Counties, TN	Gordon (1991) Ortmann (1918)	1950 1913
Big Moccasin Creek, Scott County, VA	Athearn (pers. comm., 1997) Ortmann (1918)	1963 1915, 1913
Middle Fork Holston River, Smyth County, VA[5]	Gordon (1991)	1914?
Middle Fork Holston River, Washington County, VA[6]	Gordon (1991)	~1900
South Fork Holston River, Washington County, VA[7]	Gordon (1991)	1901
South Fork Holston River, Sullivan County, TN	Ortmann (1918)	1914
Holston River, Hawkins County, TN	Ortmann (1918)	1914
Holston River, Hamblen County, TN	Boepple and Coker (1912) Gordon (1991)	1909 ~1900
Holston River, Grainger County, TN	Ortmann (1918)	1913-14
Holston River, Jefferson and Knox Counties, TN	Gordon (1991) Ortmann (1918)	<1954[2] 1913-15
French Broad River, Buncombe County, NC	Ortmann (1918)	<1913
French Broad River, ? County, TN	D. H. Stansbery (Ohio State University Museum of Zoology [OSUMZ], pers. comm., 1998)	~1886
Nolichucky River, Greene County, TN	Gordon (1991) Athearn (pers. comm., 1997)	1968 1964
Nolichucky River, Cocke and Hamblen Counties, TN	S. J. Fraley (Tennessee Valley Authority, pers. comm., 2000) Ahlstedt (pers. comm., 1997) Ahlstedt (1991a) Gordon (1991) Ortmann (1918)	2000 1997 1980 1969 1913
Little Pigeon River, Sevier County, TN	Gordon (1991) Parmalee (1988) Ortmann (1918)	1988 1985-87 1914
West Prong Little Pigeon River, Sevier County, TN	Parmalee (1988)	1985-87, A
Tennessee River, Knox County, TN	Ortmann (1918) Lewis (1870)	<1918 <1870

Stream, County, State	Authority	Date
Little River, Blount County, TN	Hatcher and Ahlstedt (1982)	1981
Little Tennessee River, Monroe County, TN	Bogan (1990)	A
Little Tennessee River, Loudon County, TN	Ortmann (1918)	<1918
Tennessee River, Meigs and Rhea Counties, TN	Parmalee et al. (1982)	A
Hiwassee River, ? County, TN[8]	Parmalee and Hughes (1994)	A
South Chickamauga Creek, Catoosa County, GA	Athearn (pers. comm., 1997)	1961, 1958
South Chickamauga Creek, Hamilton County, TN	Athearn (pers. comm., 1997)	1964
Lookout Creek, Dade County, GA	Athearn (pers. comm., 1997)	1970
Sequatchie River, Sequatchie County, TN	Hatcher and Ahlstedt (1982) Athearn (pers. comm., 1997) Gordon (1991)	1980 1955 ~1900
Sequatchie River, Marion County, TN	Athearn (pers. comm., 1997)	1958
Tennessee River, Jackson County, AL	Bogan (1990), Hughes and Parmalee (1999)	A
Paint Rock River, Jackson County, AL	Ahlstedt (1991b) Gordon (1991) Isom and Yokley (1973) Athearn (pers. comm., 1997) Ortmann (1925)	1980 1976, 1973, ~1925 1965, 1967 1957 <1920[9]
Estill Fork, Jackson County, AL	Gordon (1991)	1976, 1973, 1966
Larkin Fork, Jackson County, AL	Gordon (1991) Athearn (pers. comm., 1997)	1976 1966
Hurricane Creek, Jackson County, AL	Ahlstedt (1991b) Gordon (1991)	1980 <1920[9]
Flint River, Madison County, AL	Gordon (1991)	<1920[9]
Limestone Creek, Limestone County, AL	Ortmann (1925)	<1925
Elk River, Franklin County, TN	Isom et al. (1973) Bogan (1990)	1965-67 A
Elk River, Lincoln County, TN	Gordon (1991) Isom et al. (1973) Ortmann (1925)	1966, 1957, 1953 1965 <1920[9]

Stream, County, State	Authority	Date
Richland Creek, Giles County, TN	Ortmann (1925)	1923
Tennessee River, Colbert and Lauderdale Counties, AL	Ortmann (1925) Athearn (pers. comm., 1997) Morrison (1942), Hughes and Parmalee (1999)[10]	<1920[9] 1900 A
Shoal Creek, Lauderdale County, AL	Ortmann (1925) Athearn (pers. comm., 1997) Gordon (1991)	<1929[9] 1914 1909
Bear Creek, Franklin County, AL	Ortmann (1925)	<1920[9]
Duck River, Coffee County, TN	Isom and Yokley (1968a)	1965
Duck River, Bedford County, TN	Isom and Yokley (1968a) Bogan (1990)	1965 A
Duck River, Marshall County, TN	Ahlstedt (pers. comm., 1997) J. T. Garner (Alabama Division of Wildlife and Freshwater Fisheries, pers. comm., 1997) Shute (pers. comm., 1998) Gordon (1991) Barr et al. (1993-94) Ahlstedt (1991b) Ahlstedt (1981) Isom and Yokley (1968a) Athearn (pers. comm., 1997) van der Schalie (1973) Ortmann (1924a)	2000-01 1997, 1993-95 1991 1988, 1982 1981 1979 1976-78 1965 1956 1931 1923
Duck River, Maury County, TN	Ahlstedt (pers. comm., 1997) Isom and Yokley (1968a) Gordon (1991) Ortmann (1924a)	2000-01, <1900 1965 1937, 1891 1921-23
Buffalo River, Perry County, TN	van der Schalie (1973)	1931

[1]There is considerable conjecture concerning whether *Epioblasma capsaeformis* or *E. florentina walkeri* (or both taxa) is extant in the Big South Fork in Kentucky and Tennessee. Mantle clips have been obtained by Ahlstedt (pers. comm., 1999) of Big South Fork *Epioblasma* with the hope that molecular genetic studies will determine which taxa is represented. These records are therefore provisional.

[2]This record is based on a collection by C. Goodrich who died in 1954.

[3]These records represent data from Ahlstedt and Tuberville (1997) that was inadvertently omitted during publishing.

[4]Gordon (1991) presents a record from "Virginia, Lee County, Waldens Creek" (U.S. National Museum of Natural History [USNM] 133474) and another record as "Wallens Creek, Virginia" (University of Michigan Museum of Zoology [UMMZ] 90708). These both presumably refer to Wallen Creek, a stream from which several species are recorded by Ortmann (1918).

[5]Gordon (1991) presents this Ortmann (1918) collection record (from Chilhowie, Smyth County) as UMMZ 90700. Ortmann (1918) gives the exact same locality for *Epioblasma florentina walkeri*, a species easily confused with, but that he distinguished from, *E. capsaeformis*. This locality record for *E. capsaeformis* needs verification, as the two species rarely occur together, and no other records for *E. capsaeformis* are available for the Middle Fork.

[6]Gordon's (1991) Washington County record is based on an Adams collection that Ortmann (1918) omitted (missed?), as Ortmann's only Middle Fork records were from Smyth County, Virginia. This locality record for *E. capsaeformis* also needs verification (see Footnote 4 above).

[7]Gordon (1991) presents this record as "Holston River, Virginia, Wyeth [Wythe] Co., Barren Spring, coll. C. C. Adams" (UMMZ 90699). Ortmann (1918) listed a site where he reported *Epioblasma florentina walkeri,* but not *E. capsaeformis*, that both he (in 1913) and Adams (in 1901) collected labeled simply as "Barron" on the South Fork in Washington County. Stansbery and Clench (1978) gave Ortmann's locality as "Alvarado (Barron Station)," reiterating that both Ortmann and Adams collected at this site in 1913 and 1901, respectively. This locality therefore probably refers to the South Fork, Washington County. This *E. capsaeformis* record should also be verified (see Footnote 4 above), despite the fact that Ortmann (1918) reported it from the South Fork in Sullivan County, Tennessee.

[8]Parmalee and Hughes (1994) present this record as *Epioblasma* cf. (to be compared with) *capsaeformis.*

[9]This record is based on a collection by H. H. Smith who died in 1920.

[10]This archeological site is located near the Mississippi border, a considerable distance downstream of Ortmann's (1925) Muscle Shoals locality.

NOTE: General drainage records where specific localities were not given: (1) Bates and Dennis (1978) represents 1972 collections from Clinch River Mile 190-280 (Russell County, Virginia, to Hancock County, Tennessee); (2) Dennis (1985) represents 1972-76 collections from Duck River Mile 15-180 (Marshall to Humphreys Counties, Tennessee); (3) Dennis (1985) represents 1978 collections from North Fork Holston River (Scott County, Virginia, to Hawkins County, Tennessee); and (4) Stansbery (1973a) represents 1963-71 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee).

CODES: < = collected prior to (date); A = archeological record; R = relic shells only; and T = translocated specimens.

Table 3. *Epioblasma brevidens* occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.

Stream, County, State	Authority	Date
Cumberland River System		
Rockcastle River, Laurel, Pulaski, and Rockcastle Counties, KY	Schuster (1988) Neel and Allen (1964)	1973, 1968, 1963 1948
Cumberland River, Pulaski County, KY	Schuster (1988)	1902
Buck Creek, Pulaski County, KY	Hagman (2000) G. A. Schuster (Eastern Kentucky University, personal communication [pers. comm.], 1997) Ahlstedt and Saylor (1995-96) Gordon (1991) Schuster et al. (1989) H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997)	1998 1997 1985 1985, 1971 1975-84 1959
Big South Fork, Scott County, TN	S. A. Ahlstedt (U.S. Geological Survey, pers. comm., 2000) Bakaletz (1991)	2000 1985-86
Big South Fork, McCreary County, KY	Ahlstedt (pers. comm., 2001) Gordon (1991) Bakaletz (1991) Harker et al. (1980)	2000 ~1990 1986 1979
Big South Fork, Pulaski County, KY	Wilson and Clark (1914)	1910
Cumberland River, Wayne County, KY	Neel and Allen (1964) Wilson and Clark (1914)	1947 1910
Cumberland River, Russell County, KY	Schuster (1988) Neel and Allen (1964) Wilson and Clark (1914)	1982 R 1947 1910
Beaver Creek, Russell County, KY	Neel and Allen (1964) Wilson and Clark (1914)	1947-48 1910-12
Cumberland River, Cumberland County, KY	Neel and Allen (1964)	1947
Cumberland River, Jackson County, TN	Wilson and Clark (1914) Bogan (1990)	1910-12 A
Obey River, Clay and Pickett Counties, TN	Gordon (1991)	?
Cumberland River, Smith County, TN	Parmalee et al. (1980)	1977-79, A

Stream, County, State	Authority	Date
Cumberland River, Trousdale and Wilson Counties, TN	Parmalee et al. (1980)	1977-79
Caney Fork, Dekalb County, TN	Athearn (pers. comm., 1997)	1961 R
Caney Fork, Smith County ?, TN	Layzer et al. (1993) Gordon (1991)	~1990 R 1981 R
Caney Fork, Putnam County, TN	Wilson and Clark (1914)	1910-12
Stones River, Davidson and Rutherford Counties, TN	Schmidt et al. (1989) Gordon (1991) Johnson (1978)	1965-68 1964-65 ?
Cumberland River, Davidson County, TN [Type Locality?]	Ortmann (1924a) Johnson (1978)	~1831[1] ?
Red River, Robertson County, TN	Gordon (1991)	1966
Red River, Montgomery County, TN	Athearn (pers. comm., 1997)	1967
Cumberland River, Stewart County, TN	P. W. Parmalee (University of Tennessee, pers. comm., 1997)	A
Tennessee River System		
Clinch River, Scott County, VA	L. M. Koch (U.S. Fish and Wildlife Service [Service], pers. comm., 1997) Gordon (1991) Ahlstedt and Tuberville (1997) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997) Ortmann (1918)	1997 1990, 1929 1988, 1979 1978-83 1973-75 1968, 1965, 1953 1913, 1899
Clinch River, Hancock County, TN	R. G. Biggins (Service, personal observation) Ahlstedt and Tuberville (1997) Barr et al. (1993-94) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997)	2000, 1997 1994, 1988, 1979 1981 1978-83 1973-75 1968
Clinch River, Claiborne and Grainger Counties, TN	Ortmann (1918) Boepple and Coker (1912)	1915, 1913 1909
Clinch River, Union County, TN	Ortmann (1918)	1915, 1899
Clinch River, Anderson County, TN	Hickman (1937) Cahn (1936b) Ortmann (1918)	1935-37 1936 1914-15

Stream, County, State	Authority	Date
Powell River, Lee County, VA	Ahlstedt (pers. comm., 1997)[2] Gordon (1991) Wolcott and Neves (1994) Barr et al. (1993-94) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Ortmann (1918)	1997, 1994, 1988, 1983, 1979 1990, 1983, 1932 1988-89 1981 1979 1975-78 1973-78 1901
Station Creek, Lee County, VA[3]	Johnson (1978)	?
Wallen Creek, Lee County, VA[4]	Gordon (1991)	?
Powell River, Hancock County, TN	Ahlstedt (pers. comm., 1997) Gordon (1991) Ahlstedt and Tuberville (1997) Barr et al. (1993-94) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981)	1998, 1994 1990, 1983, 1980 1988, 1983, 1979 1981 1979 1975-78 1973-78
Powell River, Claiborne County, TN	Ahlstedt (pers. comm., 1997) Ahlstedt and Tuberville (1997) Gordon (1991) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997) Ortmann (1918)	1988 1983, 1979 1983, 1967 1979 1975-78 1973-78 1964 1915, 1913, 1899
Powell River, Union County, TN	Ortmann (1918)	1899
Powell River, Campbell County, TN	Bogan and Parmalee (1983) Johnson (1978)	? ?
Clinch River, Roane County, TN	Gordon (1991) Parmalee and Bogan (1986)	<1954[5] A
North Fork Holston River, Scott County, VA	Neves (1995) Gordon (1991) Athearn (pers. comm., 1997) Ortmann (1918)	1991-95 R 1977 1950 1913, 1901
North Fork Holston River, Hawkins and Sullivan Counties, TN	Athearn (pers. comm., 1997) Ortmann (1918)	1950 1913
Holston River, Grainger, Hamblen, and Hawkins Counties, TN	Ortmann (1918) Boepple and Coker (1912)	1913-14 1909
Holston River, Jefferson and Knox Counties, TN	Ortmann (1918)	1913-1915

Stream, County, State	Authority	Date
Nolichucky River, ? County, TN	Johnson (1978)	?
West Prong Little Pigeon River, Sevier County, TN	Parmalee (1988)	A
Tennessee River, Knox County, TN	Gordon (1991) Lewis (1870)	<1920[6] <1870
Little Tennessee River, Monroe County, TN	Bogan (1990)	A
Tennessee River, Loudon and Roane Counties, TN	Hughes and Parmalee (1999)	A
Tennessee River, Meigs and Rhea Counties, TN	Parmalee et al. (1982), Hughes and Parmalee (1999)	A
Tennessee River, Jackson County, AL	Gordon (1991) Bogan (1990), Hughes and Parmalee (1999)	? A
Paint Rock River, Jackson County, AL	Ahlstedt (pers. comm., 1997) Ortmann (1925)[7]	1976 <1914
Tennessee River, Marshall and Morgan Counties, AL	Hughes and Parmalee (1999)	A
Tennessee River, Colbert and Lauderdale Counties, AL[8]	Hinkley (1906) Ortmann (1925) Morrison (1942), Hughes and Parmalee (1999)	1904 <1920[6] A
Elk River, Lincoln County, TN	Gordon (1991) Athearn (pers. comm., 1997) Johnson (1978)	1966 1957 ?
Elk River, Limestone County, AL[9]	Ortmann (1925)	1833
Bear Creek, Colbert County, AL	McGregor and Garner (1997)	1997
Bear Creek, Tishomingo County, MS	R. Jones (Mississippi Museum of Natural Science, pers. comm., 2002) Isom and Yokley (1968b)	2002 1965
Little Bear Creek, Franklin County, AL	P. W. Shute (Tennessee Valley Authority, pers. comm., 1998)	1978
Cedar Creek, Franklin County, AL	J. T. Garner (Alabama Division of Wildlife and Freshwater Fisheries, pers. comm., 1997) Isom and Yokley (1968b)	1988 1965
Cedar Creek, Tishomingo County, MS	Isom and Yokley (1968b)	1965
Tennessee River, Hardin County, TN	Athearn (pers. comm., 1997)	<1900?

Stream, County, State	Authority	Date
Tennessee River, Decatur and Perry Counties, TN	Hughes and Parmalee (1999)	A
Tennessee River, Benton and Humphreys Counties, TN	Hughes and Parmalee (1999)	A
Duck River, Bedford County, TN	Ahlstedt (pers. comm., 2001)	2001 R
Duck River, Marshall County, TN	Ahlstedt (pers. comm., 1997) Shute (pers. comm., 1998) Ahlstedt (1981) Gordon (1991) Isom and Yokley (1968a) Athearn (pers. comm., 1997) Ortmann (1924a)	2001 R, 1988 1991 R 1976-78 1973, 1964 1965 1956, 1953 1923
Duck River, Maury County, TN	L. J. Levine (Cumberland Science Museum, pers. comm., 1997) van der Schalie (1973) Ortmann (1924a)[10] Hinkley and Marsh (1885)	1997 R 1931 1921-22 <1885

[1]The fact that Ortmann (1924a) mentions that Conrad, who was actively studying unionids in the 1830s, reported *Epioblasma brevidens* from the Cumberland River at Nashville (Davidson County), lends support to this site being the type locality.

[2]These records represent data from Ahlstedt and Tuberville (1997) that was inadvertently omitted by the publisher.

[3]Johnson (1978) includes Station Creek, Lee County, Virginia, as a tributary of Clinch River, but it is actually a tributary of the upper Powell River.

[4]Gordon (1991) presents a record from "Virginia, Lee County, Waldens Creek" (U.S. National Museum of Natural History [USNM] 133471). This presumably refers to Wallen Creek, a stream from which several species are recorded by Ortmann (1918).

[5]This record is based on a collection by C. Goodrich who died in 1954.

[6]This record is based on a collection by H. H. Smith who died in 1920.

[7]Ortmann (1925) stated that Simpson (1914) reported *Epioblasma metastriata* (Conrad 1840) from "Woodville, Alabama," which is on the Paint Rock River. As *E. metastriata* appears to be the Mobile River basin sister taxon to *E. brevidens*, this record probably represents *E. brevidens*, whose occurrence in the Paint Rock River was verified in 1976 by Ahlstedt (pers. comm., 1997).

[8]Morrison's (1942) archeological site is located near the Mississippi border, a considerable distance downstream of Ortmann's (1925) Muscle Shoals locality.

[9]Ortmann (1925) reported this species as having been collected by Conrad from the lower Elk River. The only visit Conrad made to the Elk River was in 1833 (Wheeler 1935).

[10]Ortmann (1924a) reported on central Tennessee mussel collections made by Hinkley and Marsh (1885), "[a] number of [them] from Duck River at Columbia, Maury Co., Tenn." This record probably came from this locality.

NOTE: General drainage records where specific localities were not given: (1) Bates and Dennis (1978) represents 1972 collections from Clinch River Mile 190-280 (Russell County, Virginia, to Hancock County, Tennessee); (2) Dennis (1985) represents 1972-76 collections from Duck River Mile 15-180 (Marshall to Humphreys Counties, Tennessee); (3) Dennis (1985) represents 1976-83 collections from

Cumberland River, Tennessee (counties unknown); and (4) Stansbery (1973a) represents 1963-71 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee).

CODES: < = collected prior to (date); A = archeological record; and R = relic shells only.

Table 4. *Villosa perpurpurea* **occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.**

Stream, County, State	Authority	Date
Tennessee River System		
Clinch River, Tazewell County, VA	Jones et al. (2001) Winston and Neves (1997) Ahlstedt and Tuberville (1997) Church (1991) D. H. Stansbery (Ohio State University Museum of Zoology, pers. comm., 1998) Ortmann (1918)	1998[1] 1995-96 R 1994 1989-90 1981 1912-13
Indian Creek, Tazewell County, VA	Watson and Neves (1998) Winston and Neves (1997)	1996-97 1995-96 R
Clinch River, Russell County, VA	Stansbery (1986) Ahlstedt (1991a) Ortmann (1918)	1985-86, 1965 1978-83 1913, 1899
Clinch River, Wise County, VA	Stansbery (pers. comm., 1998) Ortmann (1918)	1963 1913
Clinch River, Scott County, VA	L. M. Koch (U.S. Fish and Wildlife Service [Service], pers. comm., 1997) S. A. Ahlstedt (USGS, pers. comm., 1997) Ahlstedt (1991a) Ortmann (1918)	1997 1988, 1979 1978-83 1913
Copper Creek, Scott County, VA	Fraley and Ahlstedt (2001) Ahlstedt (pers. comm., 1997) Barr et al. (1993-94) Ahlstedt (1982) Stansbery (pers. comm., 1998)	1998 1997, 1991 1981 1980 1965, 1962 R
Clinch River, Hancock County, TN	Ahlstedt (pers. comm., 1997) Ahlstedt (1991a) H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997) Ortmann (1918)	1997 R 1978-83 1950 R 1913
Clinch River, Claiborne and Grainger Counties, TN	Boepple and Coker (1912)	1909
Powell River, Lee County, VA	Ortmann (1918)	1899
Emory River, Morgan County, TN	R. M. Anderson (USGS, pers. comm., 1998)	~1987 R
Emory River, Roane County, TN	Ortmann (1918)	1915

Stream, County, State	Authority	Date
Obed River, Morgan County, TN	Ahlstedt (pers. comm., 2001) Athearn (pers. comm., 1997) Gordon (1991)	2000 1967 ?
Obed River, Cumberland County, TN	Ahlstedt (pers. comm., 2001) Gordon (1991)	2000, 1998, 1996 ?
North Fork Holston River, Washington County, VA	Ortmann (1918)	1913
North Fork Holston River, Scott County, VA	Ortmann (1918)	1913
North Fork Holston River, Hawkins and Sullivan Counties, TN	Ortmann (1918)	1913
Beech Creek, Hawkins County, TN	S. J. Fraley (Tennessee Valley Authority [TVA], unpublished data) Ahlstedt (1982, 1991a)	1999-2002 <1982
North Fork Beech Creek, Hawkins County, TN	S. J. Fraley (TVA, unpublished data)	2001 R

[1]This record is the result of a toxic chemical spill at Cedar Bluff in the fall of 1998, which resulted in the death of approximately 250 specimens of three federally listed species, including at least 52 *Villosa perpurpurea* (see "Reasons for Decline").

NOTE: General drainage records where specific localities were not given: (1) Stansbery (1973a) represents 1963-71 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee); and (2) Stansbery (pers. comm., 1998) had a 1974 collection from the Obed River, Tennessee, which may refer to one (or both) of the Gordon (1991) records from that stream.

CODES: < = collected prior to (date); R = relic shells only.

Table 5. *Quadrula cylindrica strigillata* occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.

Stream, County, State	Authority	Date
Tennessee River System		
Clinch River, Tazewell County, VA	L. M. Koch (U.S. Fish and Wildlife Service, personal communication [pers. comm.], 1999) P. W. Shute (Tennessee Valley Authority, pers. comm., 1998) Church (1991) D. H. Stansbery (Ohio State University Museum of Zoology, pers. comm., 1998) Ortmann (1918)	1998[1] 1995 R 1989-90 R 1981 1912-13
Indian Creek, Tazewell County, VA	Watson and Neves (1998)	1996
Clinch River, Russell County, VA	Ahlstedt and Tuberville (1997) Church (1991) Stansbery (pers. comm., 1998) Ahlstedt (1991a) H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997) Ortmann (1918)	1994 1989-90 R 1985 1978-83 1967 1913
Clinch River, Scott County, VA	Koch (pers. comm., 1997) Ahlstedt and Tuberville (1997) Yeager and Neves (1986) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997) Ortmann (1918)	1997 1994, 1979 1982-83 1978-83 1973-75 1969 1913

Stream, County, State	Authority	Date
Copper Creek, Scott County, VA	Fraley and Ahlstedt (2001) S. A. Ahlstedt (U.S. Geological Survey [USGS], pers. comm., 1997) Shute (pers. comm., 1998) Ahlstedt (1982) Athearn (pers. comm., 1997)	1998 R 1991 1987-89 1980 1961, 1955
Clinch River, Hancock County, TN	R. G. Biggins (personal observation) J. T. Garner (Alabama Division of Wildlife and Freshwater Fisheries, pers. comm., 1997) Barr et al. (1993-94) Ahlstedt and Tuberville (1997) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997)	2000 1997, 1993 1981 1979 1978-83 1973-75 1968, 1956, 1950-51
Powell River, Lee County, VA	Koch (pers. comm., 1997) Shute (pers. comm., 1998) Wolcott and Neves (1994) Barr et al. (1993-94) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997) Ortmann (1918)	1997 1994, 1989, 1987 1988-89 1981 1979 1975-78 1973-78 1951 1899
Powell River, Hancock County, TN	R. J. Neves (USGS, pers. comm., 1998) Yeager and Neves (1986) Ahlstedt and Tuberville (1997) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997)	1997 1982-83 1979 1979 1975-78 1973-78 1964

Stream, County, State	Authority	Date
Powell River, Claiborne County, TN	Ahlstedt and Tuberville (1997) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Ortmann (1918)	1988 1979 1975-78 1973-78 1899
Clinch River, Claiborne County, TN	Ahlstedt (1991a)	1978-83
North Fork Holston River, Washington County, VA	Ahlstedt (1980) Ortmann (1918)	1975 T 1913
North Fork Holston River, Scott County, VA	Ahlstedt (1980) Ortmann (1918)	1975-78 T 1913, 1901
Big Moccasin Creek, Scott County, VA	Athearn (pers. comm., 1997) Ortmann (1918)	1963 1915, 1913
Possum Creek, Scott County, VA	Winston and Neves (1997)	1995-96 R
North Fork Holston River, Hawkins and Sullivan Counties, TN	Ortmann (1918)	1913
South Fork Holston River, Sullivan County, TN	Ortmann (1918)	1914

[1]This record is the result of a toxic chemical spill at Cedar Bluff in the fall of 1998, which resulted in the death of approximately 250 specimens of three federally listed species, including at least 16 *Quadrula c. strigillata* (see "Reasons for Decline").

NOTE: General drainage records where specific localities were not given: (1) Bates and Dennis (1978) represents 1972 collections from Clinch River Mile 190-280 (Russell County, Virginia, to Hancock County, Tennessee); and (2) Stansbery (1973a) represents 1963-71 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee).

CODES: < = collected prior to (date); R = relic specimens only; and T = translocated specimens.

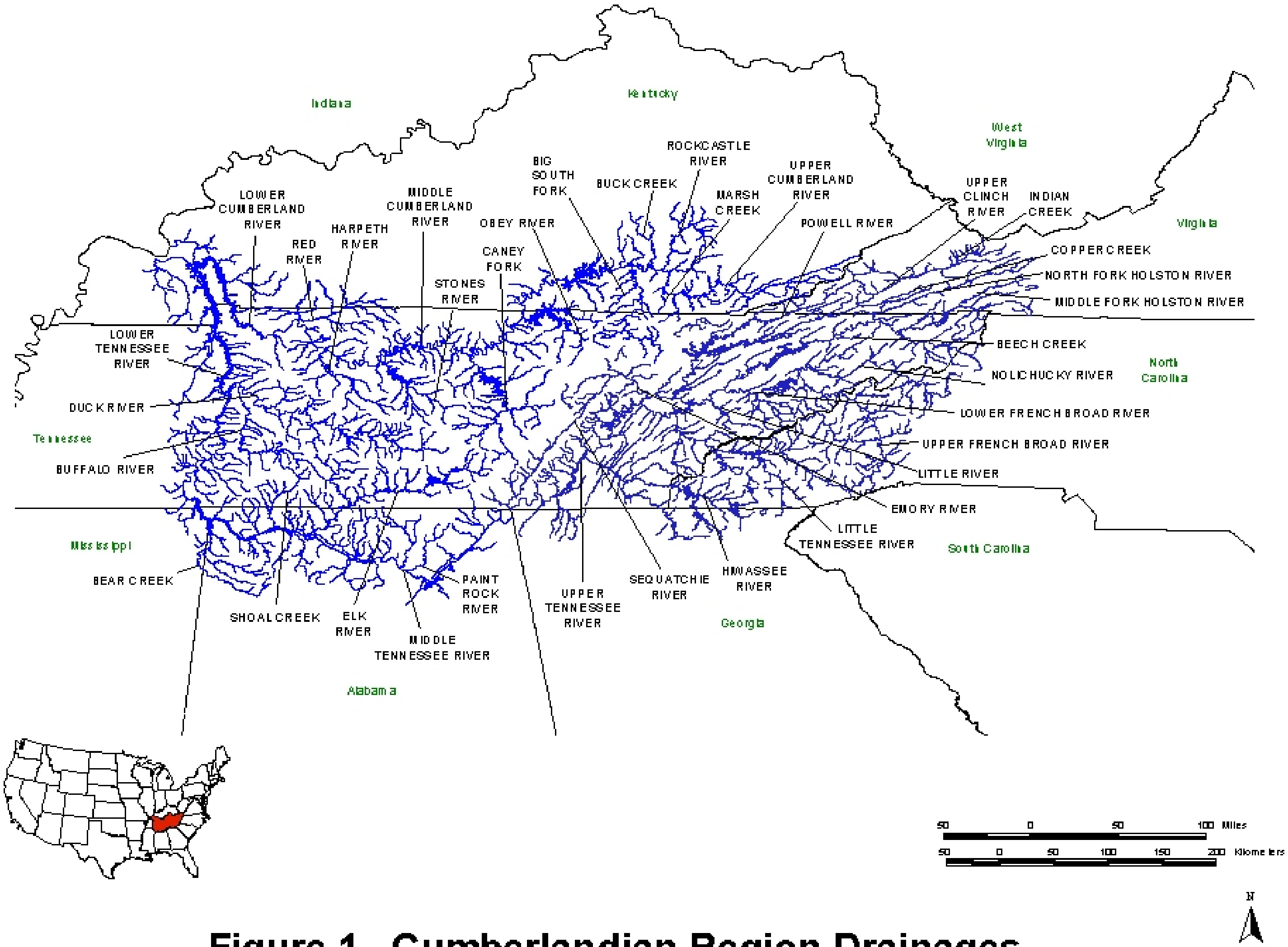

Figure 1. Cumberlandian Region Drainages

PART IV

IMPLEMENTATION SCHEDULE

Priorities in column one of the following Implementation Schedule are assigned as follows:

1. Priority 1 - An action that <u>must</u> be taken to prevent extinction or to prevent the speciesfrom declining irreversibly in the <u>foreseeable</u> future.

2. Priority 2 - An action that must be taken to prevent a significant decline in species population/habitat quality or some other significant negative impact short of extinction.

3. Priority 3 - All other actions necessary to meet the recovery objective.

<u>Key to Acronyms Used in This Implementation Schedule</u>

FA	-	Other Federal Agencies - Includes the Tennessee Valley Authority, U.S. Natural Resources Conservation Service, U.S. Forest Service, U.S. Army Corps of Engineers, U.S. Environmental Protection Agency, and Office of Surface Mining.
FWS	-	U.S. Fish and Wildlife Service
ES	-	Ecological Services Division, FWS
FI	-	Fisheries Division, FWS
LE	-	Law Enforcement Division, FWS
NGO	-	Nongovernmental Organizations (NGO; e.g., The Nature Conservancy, Tennessee Aquarium, Southeast Aquatic Research Institute, World Wildlife Fund.
R4	-	Region 4 (Southeast Region), FWS
R5	-	Region 5 (Northeast Region), FWS
SCA	-	State Conservation Agencies (e.g., Kentucky Department of Fish and Wildlife Resources, Kentucky State Nature Preserves Commission, Tennessee Wildlife Resources Agency, Tennessee Department of Environment and Conservation, Alabama Division of Wildlife and Freshwater Fisheries, Alabama Geological Survey, Virginia Department of Game and Inland Fisheries)
USDA	-	U.S. Department of Agriculture

IMPLEMENTATION SCHEDULE

Priority	Task Number	Task Description	Task Duration	Responsible Agency		Cost Estimates ($000s)			Comments
				FWS	Other	FY1	FY2	FY3	
1	1.3.6	Determine the number of individuals and sex ratio required to maintain long-term viable natural populations.	1 year	R4 and R5; ES and FI	FA, SCA, and NGO	---	---	20.0	
1	1.1	Continue to use existing legislation and regulations to protect the species and their habitats.	Continuous	R4 and R5; ES and LE	FA and SCA	15.0	15.0	15.0	
1	1.2.1, 1.2.2	Solicit help in protecting the species and their essential habitats through the development of cooperative partnerships with various entities.	Continuous	R4 and R5; ES	FA, SCA, and NGO	10.0	10.0	10.0	
1	1.2.3	Develop cooperative ventures with private landowners to restore riparian habitat through Service and USDA programs.	3 years	R4 and R5; ES	FA, SCA, and NGO	120.0	120.0	120.0	
1	1.3.1, 1.3.2, 1.3.3, 1.3.4	Conduct research necessary for species management and recovery, determine threats, and implement management actions where needed.	3 years	R4 and R5; ES and FI	FA, SCA, and NGO	50.0	50.0	50.0	

IMPLEMENTATION SCHEDULE

Priority	Task Number	Task Description	Task Duration	Responsible Agency		Cost Estimates ($000s)			Comments
				FWS	Other	FY1	FY2	FY3	
1	1.3.5	Based on the biological data and threat analyses, investigate the need for management, including habitat improvement.	3 years	R4 and R5; ES	FA, SCA, and NGO	50.0	50.0	50.0	
1	1.3.7	Conduct detailed anatomical and molecular genetic analyses of the five species throughout their ranges.	2 years	R4 and R5; ES	FA and SCA		20.0	20.0	
1	6.1	Develop a public outreach and environmental educational program using an aquatic ecosystem management and community-based watershed restoration approach.	1 year, then continuous	R4 and R5; ES	FA, SCA, and NGO	25.0	15.0	15.0	
2	2	Search for additional populations of the species and suitable habitat.	2 years	R4 and R5; ES	FA, SCA, and NGO	---	25.0	25.0	
2	2.1	Develop a prioritized list, by species, of streams and stream reaches that should be surveyed.	2 years	R4 and R5; ES	FA, SCA, and NGO	---	10.0	10.0	

IMPLEMENTATION SCHEDULE

Priority	Task Number	Task Description	Task Duration	Responsible Agency		Cost Estimates ($000s)			Comments
				FWS	Other	FY1	FY2	FY3	
1	3	Determine, through research and propagation technology, the feasibility of augmenting extant populations and reintroducing the species into historical habitat.	3 years	R4 and R5; ES and FI	FA, SCA, and NGO	20.0	20.0	20.0	
2	4	Develop and implement a program to evaluate efforts and monitor population levels and habitat conditions and assess the long-term viability of any populations.	Biennial	R4 and R5; ES and FI	FA, SCA, and NGO	10.0	---	10.0	
1	5	Develop and implement cryogenic preservation.	2 years	R4 and R5; ES and FI	FA and SCA	0	25.0	25.0	
3	7	Annually assess the overall success of the recovery program and recommend action.	Continuous	R4 and R5; ES	FA, SCA, and NGO	0.5	0.5	0.5	

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